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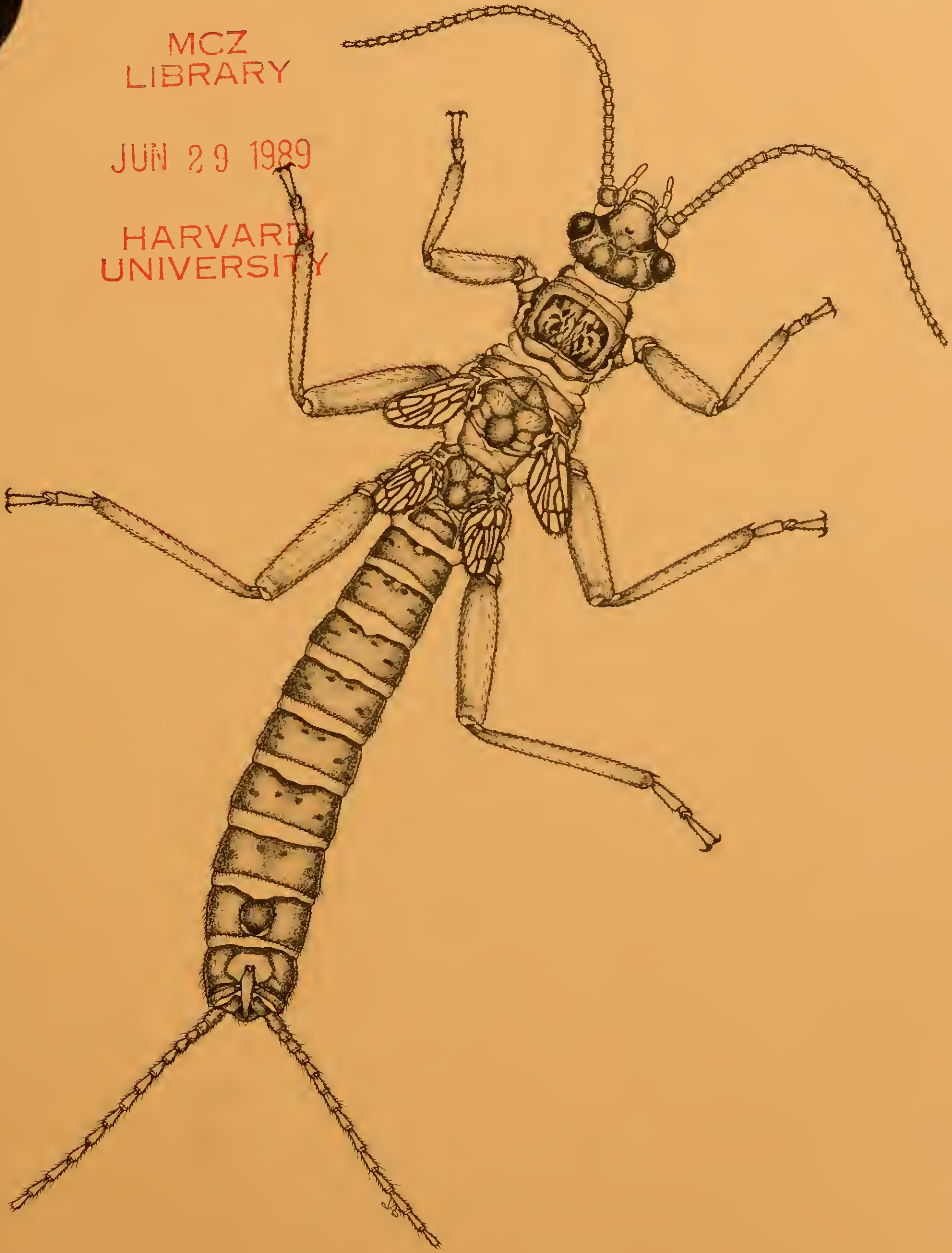

GREAT BASIN NATURALIST

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4-89 650 39866

ISSN 017-3614

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The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 49 | 31 January 1989 | No. 1

ON THE DISTRIBUTION OF UTAH'S HANGING GARDENS

Stanley L. Welsh[1]

ABSTRACT.—This is a summary monograph of the hanging gardens as they occur in the Colorado River and Virgin River portions of the Colorado Plateau in Utah. Discussed in this paper are the hanging gardens, their geography, geomorphology, aspects of distribution and diversity, and principal vascular and algal plant species. Animal trapping studies and plant productivity aspects are reviewed.

The sea of aridity that overlies southern Utah and vicinity is broken by seasonal influences and by the dendritic trenches of the Colorado River and its tributaries. The effects of the river are restricted to its banks and adjacent alluvial terraces; the riparian vegetation is generally both monotonous and predictable. Away from the riverbanks aridity is the general rule. However, here and there on the canyon walls are moist places clothed in green. They are well-watered islands in an ocean of drought (Figs. 1 and 2). It is with these patches of greenery that this paper is involved. They must be placed within their setting in order to understand the contrast of their mesophytic vegetation with the xeric communities that surround them.

The Colorado River system is entrenched into a great platform supported by a geological substructure more than a billion years old. Impressive as the inner gorges of this canyon are, the broader aspect of the system is evident to the east or south of the Wasatch Plateau in central Utah. The canyon of the Colorado at that point is more than a hundred miles wide, having yielded to the processes of erosion hundreds of cubic miles of alluvium. Despite its huge size, the canyon is of relatively recent origin, geologically speaking (Hintze 1972).

The geological strata are remarkably evident in this arid setting, where vegetative cover is thin and where rate of soil development is exceeded by processes of erosion. No great bodies of contemporary alluvium serve to obscure the underlying geology as in the Great Basin to the west. The Colorado River and its tributaries have excavated the alluvium almost as it has formed. The canyon is open to the south, and the products of erosion have been transported in the great river. Pediments of ancient erosional deposits persist for a while perched atop highlands between arms of modern drainages, but raw geological strata are exposed over huge areas of the basins of the Colorado.

Reason for the sparse protective layer of plants and for the limited soil development are related to the general aridity of the region. The dryness is a function of both low precipitation and high evaporation. Eubank (1979) records the following long-time precipitation means (in inches, followed by centimeters in parentheses) for the following stations: Hanksville 5.19 (13.18), Green River 6.06 (15.39), St. George 8.78 (22.3), Moab 8.82

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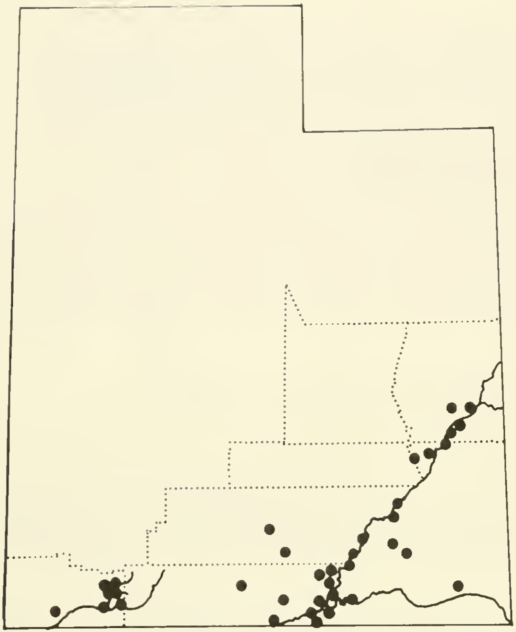

Fig. 1. Map of Utah showing distribution of hanging gardens discussed in this paper.

(22.4), Price 9.88 (25.1), Blanding 13.21 (33.55), and Zion National Park 14.61 (37.11). Mean temperatures Fahrenheit (centigrade in parentheses) for those stations are: Zion National Park 61.2 (16.2), St. George 60.1 (15.6), Moab 55.0 (12.8), Hanksville 52.3 (11.3), Green River 52.5 (11.2), Blanding 49.4 (9.7), and Price 48.8 (9.3). Extreme temperatures are probably more important than means to the survival of plants. Summer temperatures greater than 100 degrees Fahrenheit (38 degrees centigrade) are common at all of the selected stations, and winter temperatures of below zero on that scale have been recorded at all stations.

My first experience with this grandly arid country occurred almost four decades ago when I visited Glen Canyon and the townsite of Hite. I was traveling as a student in a class led by Professor Bertrand F. Harrison. No measurable rain had fallen for more than a year at the pioneer community, along the Colorado River at the mouth of Trachyte Wash, that 17th of May 1950 when I visited there.

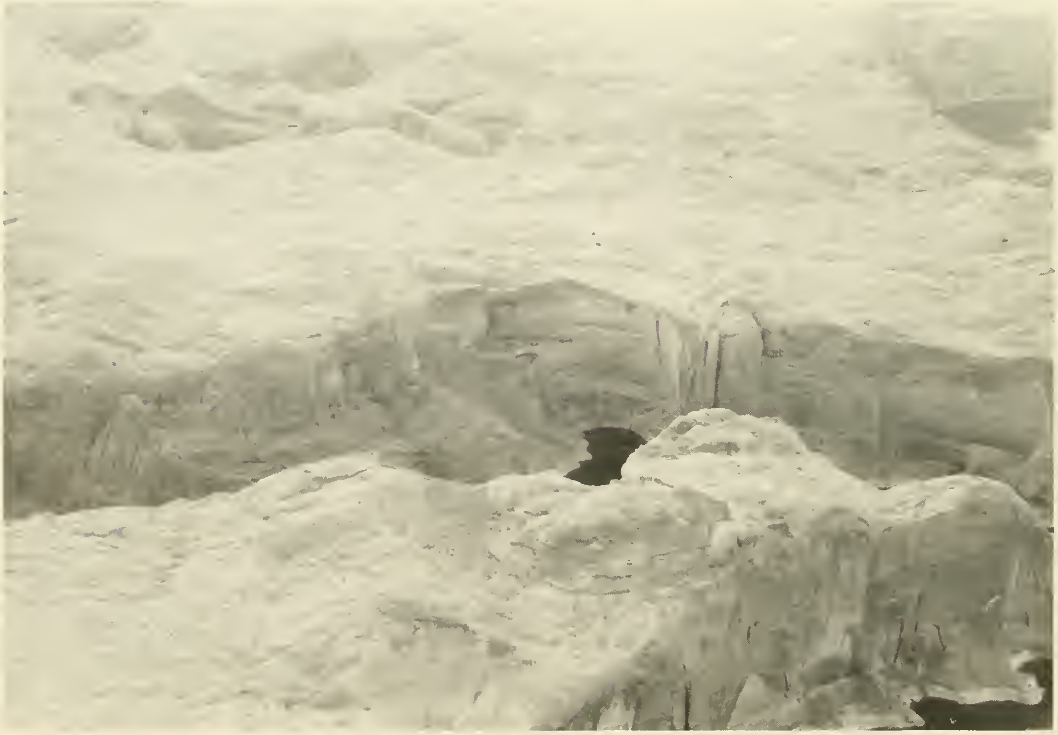

Fig. 2. Ribbon Garden, Ribbon Canyon, Lake Powell, San Juan Co., Utah. Sparingly vegetated Navajo Sandstone is cut by Glen Canyon, Ribbon Canyon, and Cottonwood Canyon.

TABLE 1. Geological strata and distributions of hanging gardens.

Geologic age	Strata	Region
Cretaceous	Wahweap	Kaiparowits
	Straight Cliffs	Kaiparowits
Jurassic	Morrison (Bluff Sst)	Bluff
	Entrada (various members)	Arches Kaiparowits Lake Powell
	Navajo Sandstone	Canyonlands Lake Powell Zion Canyon
Triassic	Navajo Sandstone	Canyonlands Zion Canyon
	Kayenta	Lake Powell St. George Zion Canyon
	Moenave (Springdale Sst)	Zion Canyon
	Chinle (Shinarump Egl)	Zion Canyon
Permian	White Rim	Canyonlands Cataract Canyon
	Cedar Mesa	Natural Bridges
Pennsylvanian	Hermosa	Cataract Canyon

Despite the aridity, there had been sufficient unmeasured water to allow for germination of some seeds, and a few diminutive plants of red brome had each matured a solitary seed, replacing those from which they had germinated. And, plants of datura displayed their huge, sweetly scented white flowers, which contrasted with the red, barren background. Prince's plume grew against a backdrop of purple siltstone, the difference in hue both pleasing and startling.

Later on that same trip to the canyon country of the Colorado, we reached Natural Bridges National Monument, where we camped. The following day we explored Armstrong and White canyons, looked at the amazing bridges, and observed the small, vertical wet seeps, occupied by mesophytic plants. This was my first introduction to the peculiar vegetative assemblages known as hanging gardens. At the time their peculiarity was lost in the immense amount of information thrust upon a student in this remarkable land for the first time.

The hanging gardens result from coincidence of water in perched bedding planes within sandstone strata intersected by the dendritic drainages of the Colorado River system (Fig. 1). The kind of garden development, whether alcove, terrace, or window-blind (Welsh and Toft 1981), is determined by the nature of the geological formation and the presence or absence of joint systems. Complexity of the plant community within a hanging garden is a function of quantity and quality of water, developmental aspects, and accessibility of plant species to it.

Hanging gardens occur in sandstone formations and sandstone members of several formations ranging in age from Pennsylvanian to Cretaceous. Massive sandstones seem to be best suited for alcove development coincidental with garden formation, some better than others. The formations with greatest development are the Navajo and Entrada, both of them cross-bedded, massive formations composed of wind-blown sand and containing ancient pond bottoms that serve as impervious bedding planes. The Wingate Formation is of similar composition but lacks significant hanging gardens. More thinly bedded sandstone formations tend not to form alcove gardens similar to those of the Navajo or Entrada. Exceptions occur, however. Main formations bearing hanging gardens are listed in Table 1.

Less than massive, though not especially bedded strata such as the Kayenta at St. George, Springdale Sandstone at Zion, and the Bluff Sandstone at Bluff, are alcove formers. The base of the alcove is not in the sandstone formation, however. Instead, the base is on the impervious formation beneath the sandstone.

The Colorado River is entrenched into geological strata that are displayed over vast regions in flat or only somewhat inclined positions. The strata are those exposed in that more or less stable geological highlands east of the hingeline in Utah (Hintze 1972). The canyons dissected into those highlands display vast sandstone surfaces along their walls. The sands of formations suitable for hanging garden development were deposited mainly on land, as dunes with interdune valleys. The interdune valleys were often the sites of lakes, whose bottoms were made impervious by accumulations of dust and other fine particles. Thin layers of limestone are evident in many of the bedding planes. Turned to stone, the ancient lake and pond basins continue to exist within the strata. Water percolating through the porous rock encounters the ancient bedding planes, still impervious and capable of holding water. When filled to overflowing, these bedding planes carry the water downward to the next bedding plane beneath or to another impervious stratum at the base of the formation.

Joint systems within the rock act as passageways for water, which follows the vertical gradient of the crack downward until it encounters some obstacle to that flow. Where the joint systems are exposed along canyon walls, the water flows over the moist surfaces. Here gardens of the windowblind type are formed. Alcove gardens develop in massive sandstones with minimal jointing. Terrace gardens result when water at the base of a stratum encounters an obstacle to its movement, flows laterally to the margin of the formation along a canyon wall, and tumbles over the terracelike margin of that impervious layer.

Flow of water from the margin of the bedding plane varies in amount from that hardly sufficient to moisten the surface of the rock to substantial quantities that collect into streams below the gardens. Many of the canyons carved in sandstone in southern Utah feature crystal-clear steams that flow perennially.

Whatever the type of garden development (alcove, terrace, or windowblind), no wet surface exists for long prior to invasion of plant propagules (Malanson 1980). Spores and dust-sized seeds are carried to the moist sites by air currents that sweep the canyons. Sticking to the moist surface, the propagules germinate to form prothallia seedlings. Algae, ferns, and seed plants are involved in community development on the wet sites.

Hanging garden formation as a geomorphological process has been discussed by Welsh and Toft (1981). The gardens are positionally unique. They tend to occur at all exposures of the canyon walls, but whatever the direction of exposure, they are shaded for much to most of each day. Indeed, some of the gardens never receive direct sunlight. A hygrothermograph placed within the Step Garden alcove along Glen Canyon recorded smooth rounded curves of temperature and humidity, as if the instrument had been placed within a house. Temperatures are moderated by the shade of canyon walls and frequently by an enclosing margin of trees and other vegetation. Air movement is restricted in well-developed gardens also, but in some they are exposed directly to both intense light and winds. Thus, there is a diversity of gardens. They vary in size, aspect, exposure to the elements, water quantity and quality, number of bedding planes, and amount of light received.

Water quality, in some degree, controls the kinds of plants in hanging gardens. Quality of water is dictated by the nature of the formations through which the water passes. Most gardens are the products of water of drinkable quality. However, water in some formations is saline and leaves a crust of various salts upon drying. In others the water is laden with calcium, which results in tufa deposits in the gardens. Generally, however, water from the gardens is potable.

Hanging garden vegetation is frequently closely juxtaposed to that of riparian plant communities immediately down the drainage. Several common components of the riparian communities occur in the gardens, but there are a series of species that are unique to this peculiar vegetative type. The unique species are more than mere extensions of the riparian vegetation. Many taxa of the gardens are widely distributed plants of diverse habitats elsewhere; others are known only from this habitat. Some of the latter, the endemics, and the distributionally unique species have taxonomic relationships with species of wide distribution in North America (Welsh and Toft 1981). Nevertheless, the plants that occupy hanging gardens are opportunists. The habitats are available to plants from specific areas, and the plants of adjacent or contemporaneously disjunct floristic regions are those that now occur in the gardens.

Hanging garden algal floras in Utah have been studied by Clark (1972), Rushforth et al. (1976), and Johansen et al. (1983). Rushforth and Merkley (1988) have published a comprehensive list by habitat of the algae of Utah. Wet walls (i.e., hanging gardens) are included by Rushforth and Merkley (1988) as one of nine habitat categories. Lists of algal species of hanging gardens cited below in Tables 2 and 3 are abstracted from the paper by Rushforth and Merkley (1988).

The small number of species known currently only from wet walls or hanging gardens might be simply an artifact of collection. They could yet be found elsewhere in subsequent collections.

Table 2. Algal components of Utah's hanging gardens.

Taxonomic group	No.	HG	1 other habitat	2+ other habitats
Cyanophyta				
Cyanophyceae				
Chrococcales	15	3	1	11
Oscillatoriales	26	4	8	14
Chlorophyta				
Chlorophyceae				
Tetrasporales	2	0	1	1
Ulotrichales	2	0	1	1
Trentepohliales	1	1	0	0
Oedogoniales	1	0	0	1
Cladophorales	1	0	0	1
Chlorococcales	3	0	0	1
Zygnematales	9	3	2	4
Chrysophyta				
Bacillariophyceae	144	5	20	119
Totals	204	16	34	154

Table 3. Hanging garden algae and distributions.

	Zion	Glen Canyon	Arches
Cyanophyta			
Gloeocapsa nigrescens Naeg.	x		
Gloeothece palea (Kutz) Rabh.	x		x
Gloeothece rupestris (Lyngb.) Born.	x	x	x
Nostoc microscopicum C. A. Ag.	x		
Oscillatoria subbrevis Schmidle f. *minor* Desik.	x		
Scytonema alatum (Carm.) Borzi		x	
Stigonema mamillosum (Lyngb.) C. A. Ag.		x	
Chlorophyta			
Trentepohlia aurea (L.) Martius		x	x
Cosmarium mineghinii Breb. var. *concinnum* Rabh.		x	x
Cosmarium undulatum Corda var. *crenulatum*			x
Zygnema sterile Trans.			x
Chrysophyta			
Caloneis alpestris (Grun.) Cl.		x	
Cymbella incerta (Grun.) Cl. var. *naviculacea* (Grun.) Cl.		x	x
Hantzschia amphioxys (Ehr.) Grun. var. *linearis* (O. Mull.) Cl.-Eul.	x		x
Mastogloea grevillei W. Sm.	x		
Pinularia biceps Greg. var. *minor* (Peters.) Cl.-Eul.	x		x

Hanging garden algae represent approximately 10.7% of the 1,900 species known from Utah. The greater proportion of the species (75%) are evidently generalists, being reported from two or more habitats besides hanging gardens. The 20 species reported from only a single habitat other than the wet walls are from lakes and reservoirs (15), not from rivers and streams, which would be more likely due to juxtaposition of the walls to those features. The others are from rivers and streams (2), thermal springs (2), and soils (1). These data might be indicative of the uniqueness of the wet wall habitat, or they might be an artifact of collection or merely an indication of commonality between species of wet walls and the great preponderance of species that occur in the lakes and reservoirs.

The current list of algae known only from wet walls in Utah and their geographic localities are given in Table 3.

Whether the apparent differences in distribution represent reality or merely lack of collection is not known. Certainly the differences noted are similar to those demonstrated conclusively for vascular plant species.

The Chyrsophyta is the largest single group of algae in the hanging gardens. The 144 species comprise 70.5% of the known algal flora. The group is represented in the gardens in greater proportion than would be expected based on the ratio of diatoms to other algae in Utah, where only slightly more than 50% of the algal flora is composed of diatoms. Evidently the wet walls present excellent habitats for diatom species.

Johansen et al. (1983) note:

> In most cases we have studied, the moist wall is inhabitated primarily by mucilage secreting green and bluegreen algae. As such species become established an abundance of secondary species colonize the mucilage. These include green and bluegreen algae and numerous diatom species as well as occasional Euglenophyta and chrysophytes.

Despite the designation as opportunists, not all plants that grow within this community type should be regarded as hanging garden species. Only those whose distribution is exclusively (or almost so) within the garden (the endemics), whose range is almost entirely from them (the elevational or spatial disjuncts), or of unusual distribution should be so categorized.

Hanging gardens are typical of the canyons of the Colorado, which occupy two main portions of Utah. They are best formed along Glen Canyon and northward to the vicinity of Moab and Arches National Park along the Colorado and Green rivers (the Canyonlands), and along the Virgin River in southwestern Utah. The gardens of the two areas are of fundamentally different structure geomorphologically. Those from along the Virgin River are best developed on the jointed walls of Zion Canyon. Alcove types along the Virgin do occur, however, especially in the Springdale member of the Moenave in Zion Canyon and vicinity, and in the Kayenta on the Red Hill in St. George. In southeastern Utah the gardens are mostly of the alcove type within poorly jointed rocks or where the jointing is not controlling the water source. Terrace gardens are present along the steplike margins of bedded sandstones such as the Wahweap and Straight Cliffs formations in western Kane County. Alcoves sometimes form in the less than massive White Rim (Cutler), Bluff (Morrison), and members of the Entrada formations. The impervious layer associated with some garden formation is the immediately underlying stratum. The Kayenta is often the layer immediately below the Navajo Formation. It acts to halt the flow of water downward, and, where intersected by a canyon, the water tumbles down its margin in a cascading, terrace garden. Above the Kayenta, huge alcoves sometimes are formed near the base of the Navajo proper (Fig. 15).

Several bedding planes are present in some alcoves (Fig. 11). Alcoves within the Navajo Sandstone are frequently more than 100 m in height. In some of them, water drips from superposed bedding planes separated by several meters of sandstone. Each of the bedding planes supports one or more of the species typical of hanging garden habitats.

The hanging garden habitat does not form a sharp boundary with the desertic vegetation externally. Some of the desertic species occur near or within the more mesic margins of the garden, and some of them are occasionally present in the gardens (e.g., species of yucca). Typically, the gardens give way gradually to plants that are more drought tolerant. Plants of intermediate moisture tolerance include a series of grass species, especially those common elsewhere in western North America on prairies and plains.

The classic alcove type of hanging garden in the Canyonlands of southeastern Utah consists of an overhanging back wall, a vaulted face wall, a detrital slope, and a plunge basin. The back and face walls support clinging plants of maidenhair fern (*Adiantum capillus-veneris* L.), cave primrose (*Primula specuicola* Rydb.), Eastwood monkey-flower (*Mimulus eastwoodiae* Rydb.), rock plant [*Petrophytum caespitosum* (Nutt.) Rydb.], and several other species. Some of these species occur also on the detrital slope, but the wet, sandy detritis supports the Garber phase of the golden sedge (*Carex aurea* Nutt.), small-flowered columbine (*Aquilegia micrantha* Eastw.), Jones reedgrass (*Calamagrostis scopulorum* Jones), helleborine orchid

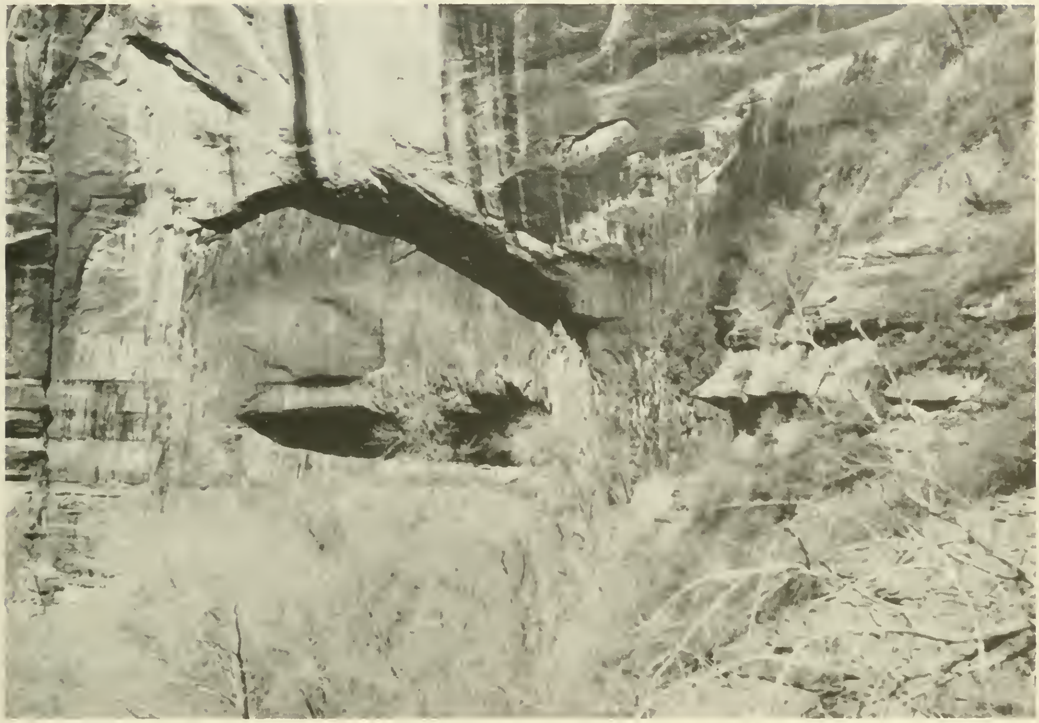

Fig. 3. Late winter view of Weeping Rock, Zion Canyon, Washington Co., Utah. Note the striated tufa deposit to the right of the main alcove. Cardinal monkey-flower and golden columbine are components of the vascular flora.

(Epipactis gigantea Dougl. ex Hook.), alcove orchid (*Habenaria zothecina* Higgins & Welsh), bundle panic (*Panicum acuminatum* Swartz), Rydberg thistle (*Cirsium rydbergii* Petrak), alcove death camas [*Zigadenus vaginatus* (Rydb.) Macbr.], and several other species also. A fringing margin of western redbud (*Cercis occidentalis* Torr. ex Gray), netleaf hackberry (*Celtis reticulata* Torr.), and Gambel and Eastwood oaks (*Quercus gambelii* Nutt. and *Q.* x *eastwoodiae* Rydb.) often occurs outward from the foot slope where the plants tend to conceal the alcove base. Toward the drier margins of the garden are grasses typical of the prairies and plains of the western United States. Little bluestem [*Schizachyrium scoparium* (Michx.) Nash in Small] is a common component, occasionally growing with Indiangrass (*Sorghastrum nutans* Nash in Small), switchgrass (*Panicum virgatum* L.), bushy bluestem [*Andropogon glomeratus* (Walter) B.S.P.], and big bluestem (*Andropogon gerardii* Vit.). The gardens tend to form a kind of microcosm of the prairies and deciduous summer forests more typical of portions of North America eastward from the Colorado Plateau.

Other species of the back and face wall of some of the alcoves are the alcove daisy (*Erigeron zothecinus* Welsh) and alcove rock-daisy (*Perityle specuicola* Welsh & Neese).

Only the cave primrose, Eastwood monkey-flower, Rydberg thistle, small-flowered columbine, alcove orchid, alcove daisy, and alcove rock-daisy are endemic to the hanging gardens of the Colorado.

Both terrace and windowblind gardens exist along the canyons of the Colorado also. Their floristic composition is frequently similar to that noted above. However, unless there is at least some alcove development, the typical garden species are lacking or occur in reduced numbers.

Hanging gardens in Zion Canyon are often of the windowblind type, with a flat face wall and a vaulted, dry arch at the top (Figs. 3–5). Sometimes the wet wall is curving and without an apparent arch at the top. The joints are mostly evident as cracks that can be seen between the dry capstone arch and the smooth

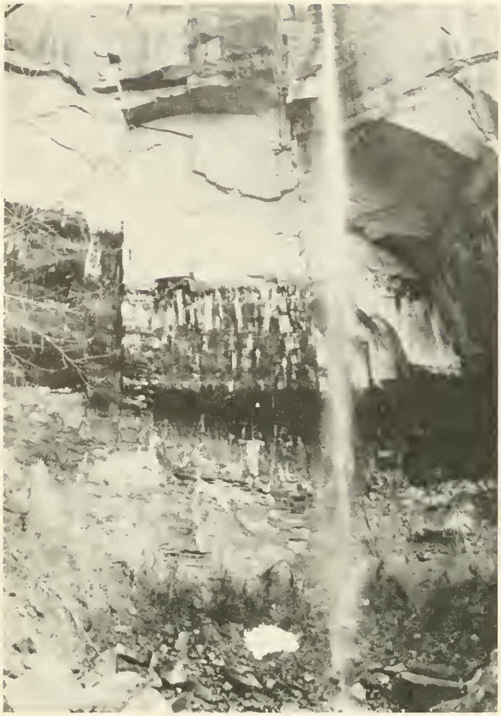

Fig. 4. Late winter view of Upper Emerald Pool Garden, Zion Canyon, Washington Co., Utah. A snowbank persists in the foreground. Joints in the Kayenta Sandstone control water flow.

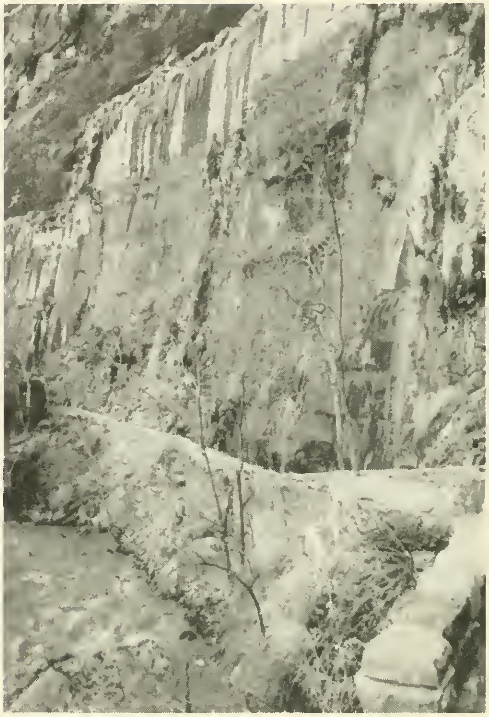

Fig. 5. Late winter view of Narrows Trail Garden, Zion Canyon, Washington Co., Utah. This garden supports the Zion shooting-star, maidenhair fern, yellow columbine, and western columbine.

face wall, but they are markedly apparent as vertical cracks in the rock faces of gardens such as those at Upper Emerald Pool. Alcove development does occur to some extent within the windowblind gardens (Fig. 6), and alcoves are present below the Springdale Sandstone member of the Moenave Formation (Fig. 7). There are no classic alcove gardens in Zion Canyon. Lack of classic alcoves can be attributed to the control of downward movement of water along the joint systems in the Navajo Sandstone, which is sometimes transitional into the bedded Kayenta Formation. Alcove development within the windowblind gardens is minimal, due in part to the peculiarity of climatic conditions within Zion Canyon. Narrow, deep, and shaded for much of each day, more so than the gardens of Canyonlands, the windowblind gardens of Zion Canyon have low winter temperatures that result in ice formation over the wet surfaces of the gardens. Moderating weather results in ice melt. Sheets of ice cascade from the cliff face, shearing plantlets clinging precariously to the stone. The attachment fails prior to building up an accumulation of detritis and prior to creation of minor indentations in the rock surface. Alcove development is slowed.

Trees adjacent to the wet walls of Zion Canyon are etiolated as a result of shading through much of each day. The long, slender branches of many trees are unable to support the weight of the crown and break under the stress. Proportionally, the trees are too tall for the thickness of the trunks.

Even the alcove at Weeping Rock is not well developed (Figs. 3, 6). Ice forms on its flat upper surface also, during some winters at least. And, though water from its aquifer is abundant during late winter and spring (Fig. 6), the water flow diminishes during early summer, and the garden is often merely damp during late summer and autumn. Tufa deposits in the Weeping Rock garden provide microhabitats where plants are protected from erosion by ice. Tiny caverns and depressions beneath overhanging tufa accumulations

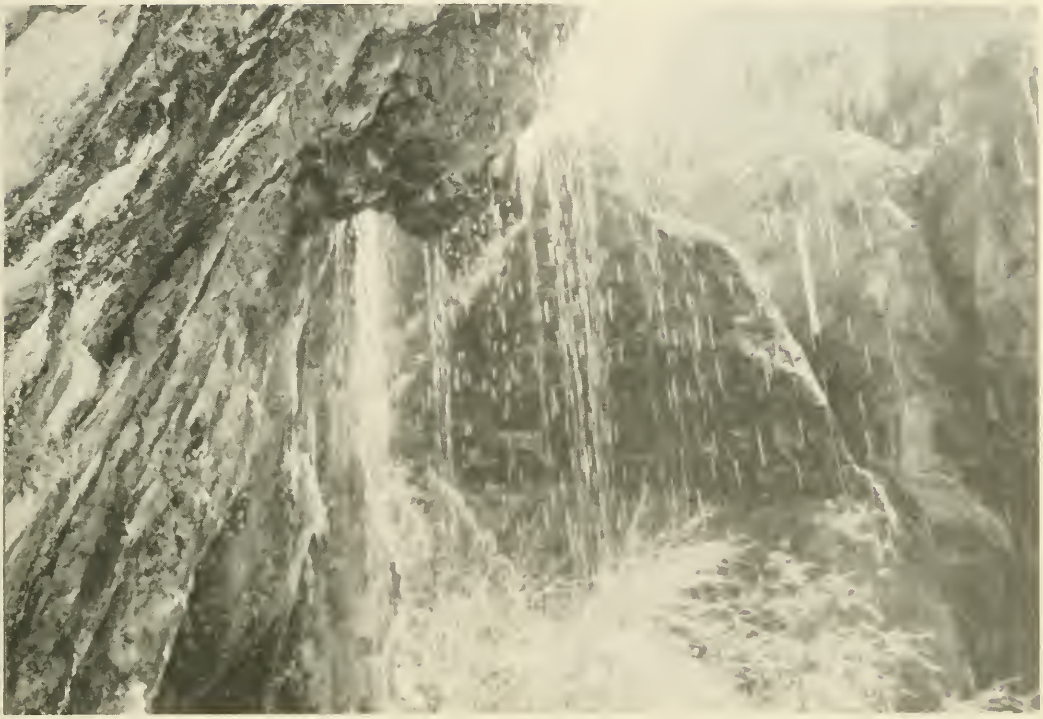

Fig. 6. Late winter view south from the alcove of Weeping Rock, Zion Canyon, Washington Co., Utah. Water drips abundantly from the tufa deposit and sandstone walls early each year but dries as the season progresses.

support miniature gardens. The tufa deposits also protect the alcoves from exfoliation, which is apparent in the north portion of Weeping Rock where tufa is absent.

Clinging plant species in the Zion Canyon gardens tend to be few in number (Malanson 1980, 1982, Malanson and Kay 1982). Fewer still are coincidental species with the hanging gardens of the Colorado. Jones reedgrass (*Calamagrostis scopulorum* Jones), Garber sedge (*Carex aurea* Nutt.), and maidenhair fern (*Adiantum capillus-veneris* L.) are present in gardens of both places. Northern maidenhair fern (*A. pedatum* L.) is present also in some gardens in Zion Canyon but is missing in all Colorado gardens except for a few near the head of the Escalante drainage. Mostly the representation within the Zion gardens is congeneric, not conspecific, with that of the Canyonlands. Columbine (*Aquilegia*) is present in both areas, but that of the Colorado is *Aquilegia micrantha* Eastw., while those of Zion Canyon are *A. formosa* Fisch. in DC. and *A. chrysantha* Gray and their hybrids. A peculiar phase (var. *fosteri* Welsh) of *A. formosa* simulates *A. micrantha* in being glandular overall, but the plant is obviously allied to *A. formosa*.

Red-flowered species of monkey-flower occur in gardens of both areas, but the species are different. That of the Canyonlands is *Mimulus eastwoodiae* Rydb., while that of Zion is *M. cardinalis* Dougl. ex Benth. (including *M. verbenaceus* Kearney & Peebles). Eastwood monkey-flower is evidently confined to the hanging garden habitats of the Colorado Plateau, while the cardinal monkey-flower is a disjunct garden plant only at the northern limits of its distribution in Zion Canyon. Otherwise the cardinal monkey-flower is a widespread species of moist sites of the Southwest. The two species likewise differ in flowering time. The plant of the Colorado gardens flowers from August to October or even to November in some years. The Zion plants have an initial flush of flowering in May and June, with fewer flowers produced thereafter into the summer months.

The cave primrose (*Primula specuicola* Rydb.) of the Canyonlands gardens has a confamilial representative in Zion, i.e., the beautiful, broad-leaved shooting-star, *Dodecatheon*

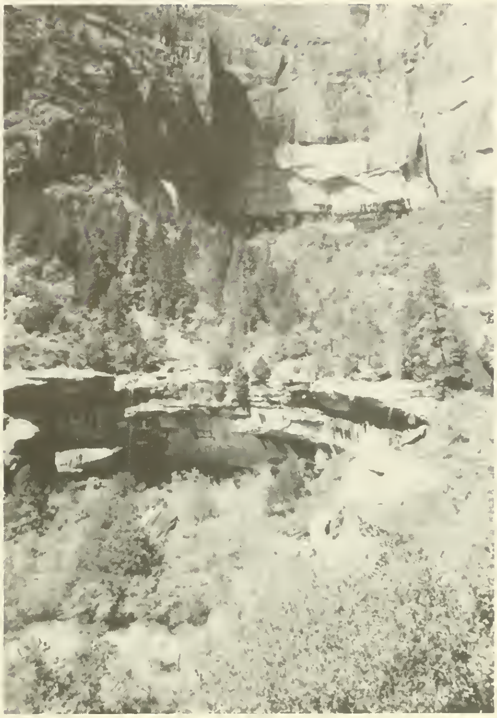

Fig. 7. Lower and Upper Emerald Pool gardens, Zion Canyon, Washington Co., Utah. The upper garden is in Kayenta Sandstone, the lower in the Springdale member of the Moenave Formation.

pulchellum (Raf.) Merrill var. *zionense* (Eastw.) Welsh. While both the cave primrose and the Zion shooting-star begin growth and flower early, the cave primrose is the more precocious, flowering as early as late January in some years. The typical period of main flowering is March to May. The Zion shooting-star seldom flowers prior to early April, with greatest flowering occurring during May. The genus *Primula* per se is not known in Zion. The Zion variety of the pretty shooting-star extends into some minor gardens along the Colorado, especially in those of lower Last Chance Canyon east of Wahweap and in selected gardens as far north as the mouth of the Escalante along Glen Canyon.

Zion Canyon has other species unique to Utah hanging gardens. American spikenard, *Aralia racemosa* L. ssp. *bicrenata* (Woot. & Standl.) Welsh & Atwood, is perhaps the most peculiar of Zion hanging gardens species. It is typically present on margins and lower shelves below the great wet walls. Occasionally it clings, attached in crevices, to the walls of the grottos associated with the gardens, and seldom the plants grow on sandy benchlands and terraces in the Narrows portion of Zion Canyon, removed from the gardens altogether. The spikenard occasionally grows to a height of almost 2 m and has ternate-pinnate leaves to almost 1 m in width. The Zion daisy, *Erigeron sionis* Cronq., is an endemic of moist sites in Zion Canyon. Habitats of the Zion daisy vary in size from minute areas, wet only in springtime by water percolating shallowly in sandstone, to the largest of the hanging gardens in the canyon. Growth of this attractive small plant with white flowers and lobed leaves is aided by production of stolons that bind the plant closely to the moist, sandy surface.

Grasses typical of prairies and plains, such as occur within and on the fringes of gardens of the Colorado, seldom form such stands in Zion Canyon. Many of the same species occur in the vicinity, but in Zion they are typically riparian components.

Hanging gardens occur on the red sandstone cliffs immediately north of the business district of St. George, Utah. These gardens are exposed to direct sunlight through much of each day, except where the alcoves are sufficiently developed to provide shade in early morning and late afternoon. Maidenhair fern (*Adiantum capillus-veneris* L.) is a principal component of these gardens also, but the bright flowers of columbine, primrose, and shooting-star are missing. Instead, the blue flowers of *Sisyrinchium demissum* Greene grace these gardens. The thistle species, *Cirsium virginensis* Welsh, grows in them but is not confined to this habitat. *Solidago spectabilis* (D.C. Eaton) Gray, the Nevada goldenrod, is an opportunist in the St. George gardens. The gardens have served as dumping grounds for residents of the region and contain old refrigerators, tires, washing machines, and other refuse, a kind of permanent condemnation of the humanity of our time.

The examples discussed here give an indication of the importance of position and ecology in the determination of garden diversity and species composition. Not indicated is the variation from place to place within a major drainage system or from garden to adjacent garden at a given place.

VIRGIN RIVER GARDENS

Hanging gardens are present at St. George, in Zion Canyon along the North Fork of the Virgin River, and along Parunuweap, a canyon cut by the main fork of the Virgin. The largest and best developed are those of Zion Canyon, described above. The Parunuweap gardens are mainly associated with the base of the Springdale Sandstone, and they are generally small and lack the diversity of those in Zion Canyon. Eastward in Parunuweap the canyon is incised into the Navajo Sandstone, and gardens are larger and better vegetated.

The Virgin thistle (*Cirsium virginensis* Welsh) was described from plants of the alcoves at the north margin of St. George. The species was first taken, evidently, by Charles Christopher Parry during his visit there in 1874 (Welsh 1988). Subsequently, the plant was collected by other botanists but remained unnamed until this decade (Welsh 1982). The thistle is evidently a riparian species, which reaches its northernmost distribution in these hanging gardens. The plant is known otherwise from moist habitats in adjacent Mohave County, Arizona, and Clark County, Nevada.

COLORADO RIVER CANYONS GARDENS

Glen Canyon

There is a land that was
That we who are can never see
For it is drowned
In crystal waters of a
Stone-bound inland sea—
Glen Canyon

SLW, Goldfield, Nevada, 2 April 1982

Moist spots on the canyon walls immediately downstream from Glen Canyon Dam support hanging garden species. These can be viewed by looking almost vertically into Glen Canyon from the visitor center of the recreation area. They are only an indication of the gardens to the east along Glen Canyon proper in Utah.

Glen Canyon was named by John Wesley Powell, who entered it on 29 July 1869 (Powell 1875). Powell (1875) states:

> On the walls, and back many miles into the country, a number of monument-shaped buttes are observed. So we have here a curious ensemble of wonderful features—carved walls, royal arches, glens, alcove gulches, mounds, and monuments. From which of these shall we select a name? We decided to call it Glen Canyon.

On 3 August 1869, Powell (1875) gave the following description:

> Sometimes the rock are overhanging; in other curves curious narrow glens are found. Through these we climb by a rough stairway, perhaps several hundred feet, to where a spring bursts out from under an overhanging cliff and where cottonwoods and willows stand, while along the curves of the brooklet oaks grow and other rich vegetation is seen, in marked contrast to the general appearance of naked rock. We call these Oak Glens.

Thus, Powell not only chose to name the canyon after the glens observed in its length, but he gave a general description of these unique botanical features. The oak glens are now known as hanging gardens.

Glen Canyon, which begins at the confluence of the Dirty Devil River and the Colorado, near the Hite Bridge, and terminates at Lee's Ferry in Arizona, is readily divisible into the following three main segments.

Wahweap to Confluence of the San Juan

Vegetation along the shores of Lake Powell from Wahweap eastward to Rock Creek and vicinity is composed mainly of species of shrubs, perched atop sands derived from the Navajo and Carmel formations. North of the lake the Entrada forms cliffs below the escarpments carved into the soft Tropic Shale member of the Mancos Shale. The Entrada changes appearance east from Wahweap; at Padre Bay it has become a candy-striped to red sandstone, instead of the chalky white, stained brown cliff former at Wahweap Bay.

Small hanging gardens of the terrace type are in Crosby Canyon, a minor tributary of Warm Creek. Other similar terrace gardens are present in Last Chance Canyon, which intersects bedded portions of the Entrada. A small garden at Nipple Spring on Nipple Bench, north of Big Water (formerly Glen Canyon City), includes maidenhair fern in a tiny, well-watered alcove in the Straight Cliffs formation. Excess water supports Fremont cottonwood and other riparian plants (Fig. 8). Water quality in these formations is generally saline, and white encrustations of salts are commonplace. Zion shooting-star is a component of the gardens, which support large stands of little bluestem. Etiolated, sprawling plants of roundleaf buffaloberry (*Shepherdia rotundifolia* Parry) and skunkbush (*Rhus aromatica* Ait.) sometimes persist in minor alcoves in this formation. These gardens have not been studied in detail.

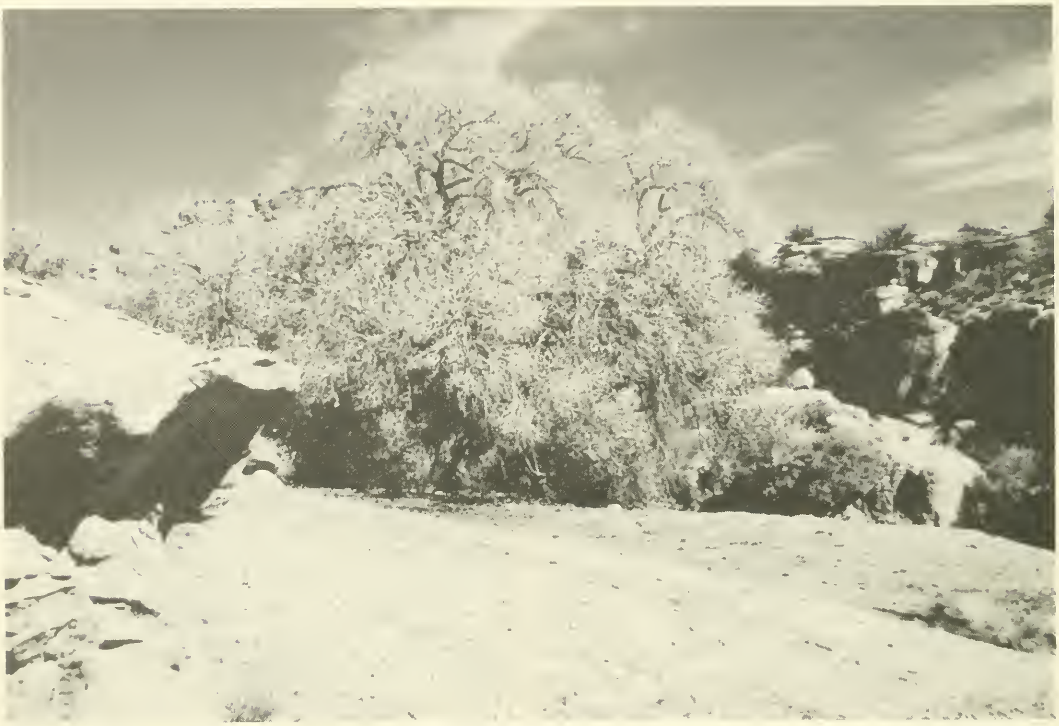

Fig. 8. Nipple Spring, Nipple Bench, Kane Co., Utah. Water from the Straight Cliffs Formation supports a small hanging garden of maidenhair ferns and gives moisture that allows growth of Fremont cottonwood.

There are some small gardens in the red, pockmarked phase of the Entrada in the Rock Creek vicinity. Others in that formation were inundated by Lake Powell. The best developed of the hanging gardens remaining in this sector of Glen Canyon are to the east of Dangling Rope, where the Navajo Formation reappears at the water's edge. Possibly the best examples are those in Driftwood Canyon, whose backdrop to the north is the great gray, water-stained cyclorama of cliffs below the summit of Fifty-Mile Mountain. On the east side of Driftwood Canyon, around the first meander bend north of its mouth, are the remains of a small but unique plant assemblage known as Step Garden. For the sake of reference the hanging gardens studied previously by this author have been given binomials, not unlike those used scientifically for plants.

Step Garden received its name from the historic steps, now beneath the lake, carved by optimistic early prospectors in search of gold in ancient terrace gravels perched high above the present inner gorge.

Though small, Step Garden is almost unique among hanging gardens in Glen Canyon in supporting a stand of saw-grass [*Cladium californicum* (Wats.) O'Neil in Tidestr. & Kittel]. This saw-grass, a close relative of the warm temperate and subtropical *C. mariscus* R. Br. with which it is sometimes united as a variety, grows here in huge clumps. The accumulated bases beneath the current seasons of growth are now more than 2 m thick. A sample of leaf bases from near the bottom of the accumulation was radiocarbon dated at more than 400 years in age. The saw-grass is unusual in Utah, reaching its northern limits here. The species grows also along Furnace Creek in Death Valley, California. In the broad sense of *C. mariscus*, the species is known from California, Nevada, Arizona, Mexico, Central America, eastern North America, and the Old World (Munz 1970). In Step Garden the saw-grass occurs with western redbud, another species of broad distribution to the south and west of Glen Canyon.

The alcove at Step Garden is very small, only about 3–5 m in height. It has an overhanging upper ledge, whose underside is clothed with maidenhair fern and Eastwood monkey-flower. The face wall has more maidenhair fern, rock plant, and helleborine orchid. A small plunge basin, scoured by water that pours over the cliff margin from a drainage above, is filled with cool water that seeps from the sandstone of the alcove. The alcove was formed from interaction of plants and the wet surface at the margin of a small bedding plane almost at the base of the Navajo Sandstone. Such alcoves are a dominant feature of this portion of Glen Canyon, and it is suggested that all alcoves along the canyon, whether now vegetated or not, are the result of previous hanging garden and wet bedding plane interaction.

There is a developmental sequence in hanging garden and alcove development from a simple wet wall or wet spot on a wall, to a simple alcove without a plunge basin, to a classic alcove with a plunge basin (Welsh and Toft 1981). A final category of alcoves is that designated as decadent, those in which the alcove has become too deep and the roof has collapsed, sealing the moisture of the bedding plane or those in which the bedding plane has dried.

Step Garden is a small classic alcove, sheltered in front from the searing heat of the sun and from wind action by a cluster of redbud and the growth of saw-grass. The plunge basin at Step Garden is sheltered behind the wall of redbud. In some gardens the plunge basin is unvegetated, the falling water from seasonal storms or from melting snow scouring the basin into bedrock. However, in some classic gardens the plunge basin is in accumulated sandy detritis from both the falling water and exfoliation of the alcove. In those situations the plunge basin will be surrounded by mesophytes such as seep willow (*Baccharis* spp.), bushy bluestem, alcove death camas, and various sedges.

Pot sherds adjacent to Step Garden and other gardens with plunge basins suggest their importance as sources of water for prehistoric peoples. Pipelines and water cisterns of contemporary civilization are prominent features of hanging gardens in St. George and in Zion National Park.

Water in the gardens is utilized by animals of many kinds (Welsh, Wood, and Raines 1975). Birds drink the water and roost and nest in the vegetation. And, since the water supply of the gardens is more or less independent of the climatic regime of the region, plant growth in them is independent of current annual rainfall. There is vegetation in abundance each year (Welsh and Wood 1975). Because of the productivity of the gardens, several species of small desert mammals survive in them during periods of less than adequate rainfall in the sea of aridity abounding beyond the gardens proper. Woodrats and deer mice especially live in the gardens during periods of climatic stress and move outward from them during seasons of adequate moisture and concurrent vegetative growth in the surrounding desertic lands (see discussion under Three Garden below).

Canyon tree frogs (*Hyla arenicolor* Cope) and red-spotted toads (*Bufo punctatus* Baird & Girard) congregate in the plunge basins of the gardens and in canyons with permanent streams (Toft 1972). They begin to call as evening falls, often accompanied by the dying calls of a canyon wren, with its lilting song that begins high and falls gradually prior to ceasing. In spring and early summer croaking of the frogs and toads rises to an amazing cacaphony soon after nightfall, often magnified by the vaulted arch of a hanging garden alcove.

Eastward from Driftwood Canyon, on the south side of the lake, is Forbidding Canyon, which contains Rainbow Bridge, sculpted from Navajo Sandstone and perched on shelfrock of Kayenta Formation, an impervious sandstone. A stream channel bearing perennial water is entrenched into the Kayenta at Rainbow Bridge. The Kayenta supported several small hanging gardens prior to flooding by Lake Powell. Plants of Toft yucca occur on sand adjacent to the bridge, and western redbud grows here and there against the cliffs, watered by runoff from the slickrock.

Not far west from the confluence with the San Juan Arm, Hidden Passage Canyon enters Glen Canyon from the west. Its walls are vertical and the canyon is short, ending abruptly in a boxed end. Along the canyon, at the base of vertical cliffs atop rounded sandstone slopes that drop to the water, are a

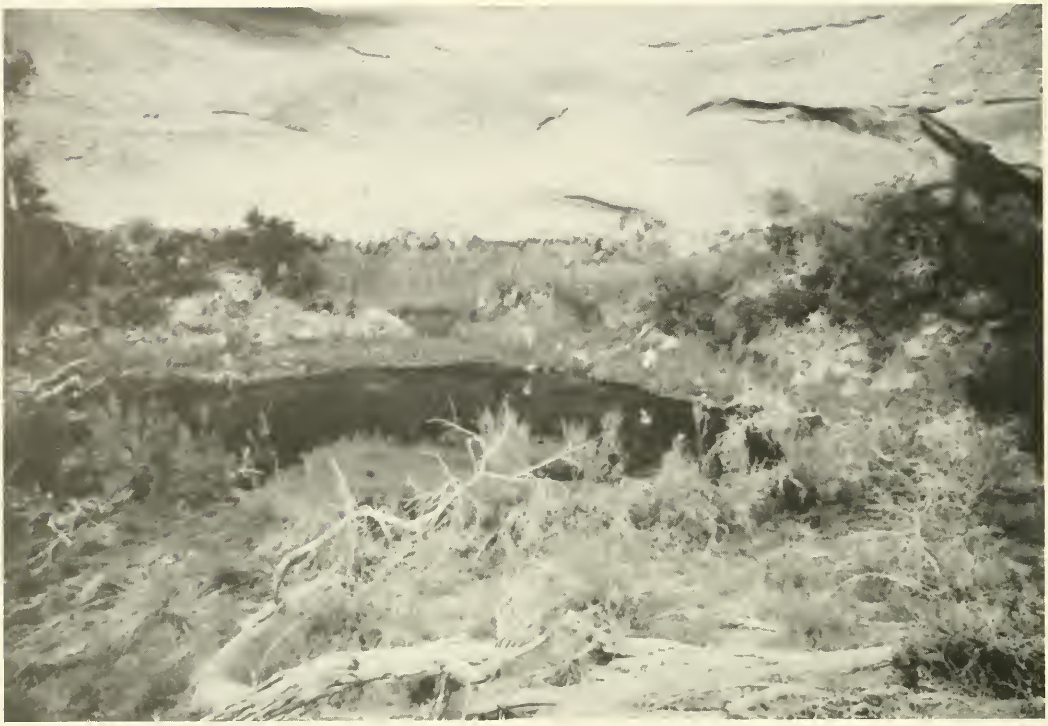

Fig. 9. Plunge basin and lower bedding plane at Pool Garden, Reflection Canyon, Lake Powell, Kane Co., Utah. This garden now lies beneath Lake Powell. Sheathed death camas grew on the wet wall, and the plunge basin, more than 15 m in width, served as home for beavers.

couple of clumps of saw-grass, a portion of what existed prior to the high water of Lake Powell.

Across the lake from the mouth of Hidden Passage is Music Temple Canyon, or what is left of it. The canyon mouth plunged for more than 100 feet into a huge alcove or grotto, elongated oval in form. The walls were clothed in part with patches of maidenhair fern and monkey-flower. It was in this grotto that Powell (1875) and his party encamped. Powell noted:

> On entering, we find a little grove of box-elder and cottonwood trees, and turning to the right, we find ourselves in a vast chamber, carved out of the rock. At the upper end there is a clear, deep pool of water, bordered with verdure. Standing by the side of this, we can see the grove at the entrance. The chamber is more than 200 feet high, 500 feet long, and 200 feet wide. Through the ceiling, and on through the rocks for a thousand feet above, there is a narrow, winding skylight. . . . It was doubtless made for an academy of music by its storm-born architect; so we name it Music Temple.

To the north of Music Temple Canyon, across Lake Powell, is Reflection Canyon, certainly one of the most photogenic tributaries of Glen Canyon. Interlocking canyon spurs now plunge into the placid waters of the lake, giving reflections that deceive the mind—air passes into water without perception of the difference in state of matter. Some of the meander bends contain remnants of hanging gardens. One such garden, named Reflection (Fig. 9), had an alcove more than 60 m in height and breadth. A plunge basin more than 15 m across served as home for a family of beavers. Alcove death camas, bearded bluestem, and seep willow grew around the plunge basin and on the foot slope of this enormous garden. The wet wall of this and of most other gardens was covered by a mat of green and blue-green algae, often with globes of *Nostoc* staring eyelike from the glistening algal mat (Clark 1972, Rushforth et al. 1976). Now the lower portion of the garden is flooded, including the plunge basin, a part of Lake Powell. The beaver have moved up canyon in pursuit of cottonwood trees, their main source of food.

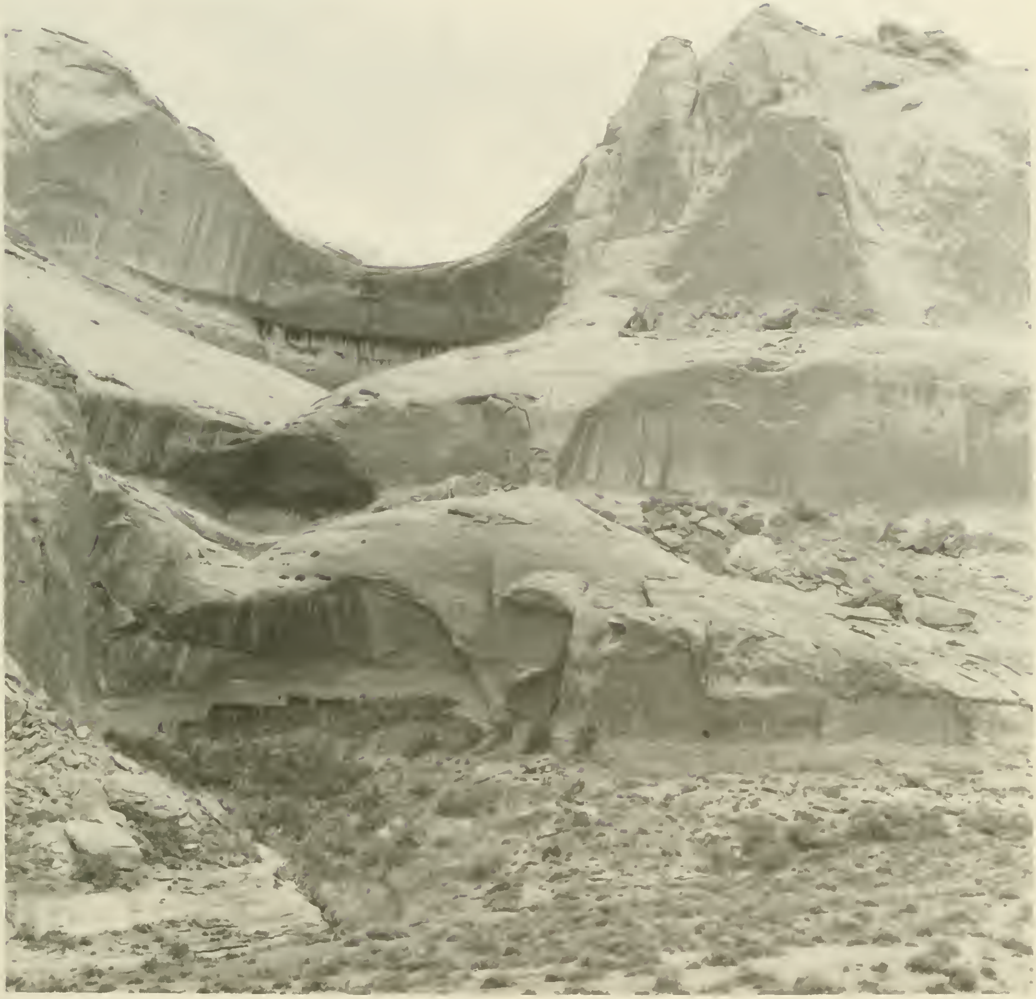

Fig. 10. Three Garden, ca 1.5 km north of the confluence of the San Juan and Glen Canyon arms of Lake Powell, San Juan Co., Utah. This superposed set of gardens was selected for study of species composition, cover, productivity, and rodent interaction. Lake Powell now covers the lower garden up to the vegetated stripes on the face wall.

San Juan Confluence to Bullfrog

North of the confluence of Glen Canyon with the San Juan, on the east side of the lake, is an area designated as Gardens Cove. Several small hanging gardens existed in this area, and a large one, designated as Three Garden, is present at the north end (Fig. 10). Three Garden was named for its three superposed alcoves, each with hanging garden development. It was a classic set. The lowermost garden had a plunge basin, a lower shelf, a gently angled foot slope, a rounded, arching face wall, and an overhanging back wall, with all of the plant components noted previously. It became the type with which all other gardens were compared by me in later studies. The basal two-thirds of the lower garden is now drowned, but Middle and Upper gardens persist. The two upper gardens can be reached by judicious scrambling up slickrock. Middle Garden is dryish, with a pothole arch in its back wall. Upper Garden (Fig. 11) is huge, with a scoured shelf where a plunge basin might develop. Down the drainage toward the lip of the overhanging margin of Middle Garden are a series of swirl holes carved into the stone, one of which became the pothole arch.

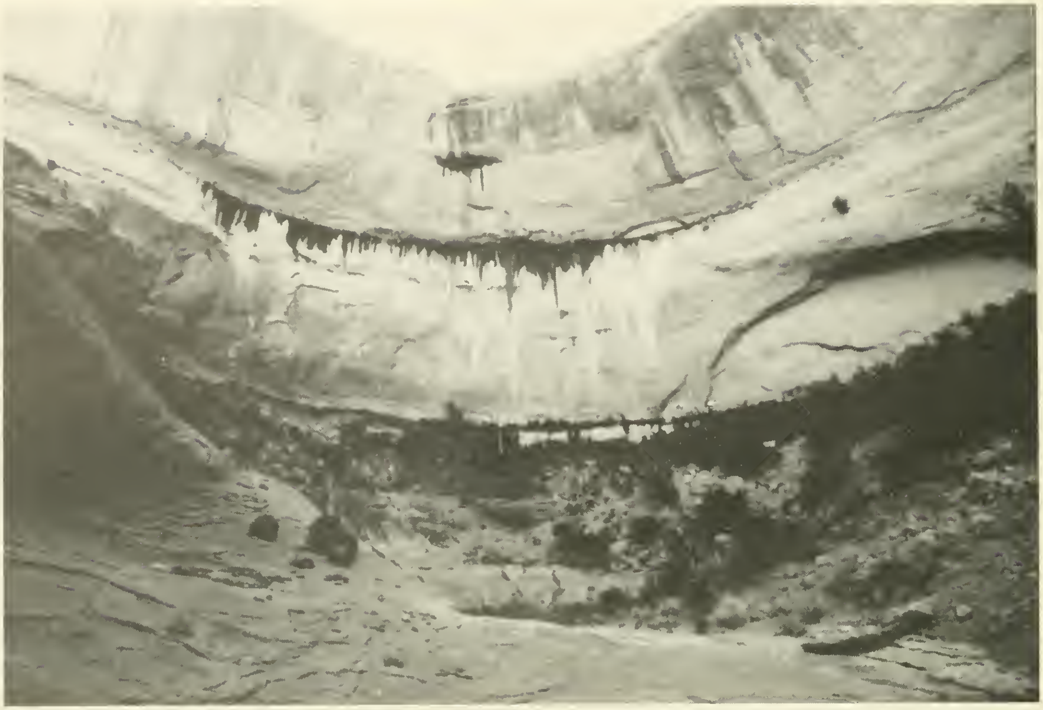

Fig. 11. Upper Three Garden, with two upper bedding planes and a larger basal one, Navajo Sandstone, San Juan Co., Utah. Water drips from the bedding planes at all seasons.

At Three Garden we undertook investigations of small mammal populations (Welsh and Toft 1972, Welsh, Wood, and Raines 1975) and studied the use of the gardens by rodents especially. Three groups of rodents were found in or near the garden habitats. They are the cricetids, heteromyids, and sciurids. Cricetid rodents include the native rats [*Neotoma cinerea* (Ord) and *N. mexicana* (Baird)] and deer mice [*Peromyscus boylei* (Baird) and *P. crinitus* (Merriam)]; the heteromyids are the kangaroo rats [*Dipodomys ordii* (Woodhouse)] and pocket mice [*Perognathus apache* (Merriam) and *P. intermedius* (Merriam)]; and the sciurids are the antelope ground squirrel [*Ammospermophilus leucurus* (Merriam)] and chipmunk [*Eutamias quadrivittatus* (Say)].

The cricetid and heteromyid rodents are nocturnal animals who forage at night and sleep in burrows during the daytime. The sciurids are diurnal. The trapping design was primarily for the nocturnal animals. Traps were opened and baited in early evening, and the traps were checked and the animals released prior to sunrise. Inclusion of the sciurids in the traps at all represented chance occurrences of late afternoon or early evening visitation.

Three principal habitats occurred in the vicinity of the gardens, i.e., the gardens proper (HG), the immediately adjacent talus (TDS) slopes dominated by sparse cover of shrubs and grasses, and a semidesert shrub (SDS) on the more gently sloping, sandy ground away from the garden and talus slopes. The hanging garden habitat was tested in the summer of 1972 (Welsh and Toft 1972) to determine species presence and potential of movement from garden to garden in the superposed set. Animals moved from Middle to Lower Garden during the three-night test trapping. In 1973 and 1974 a larger trapping design was imposed on the HG, TDS, and SDS communities. Results of those studies indicated that there was a partitioning of habitat by species of the three rodent groups. Heteromyids avoided the gardens altogether (except for *Perognathus intermedius*, which lives almost exclusively in the adjacent TDS habitat). Sciurids visited the gardens probably for food and occasionally for water, even

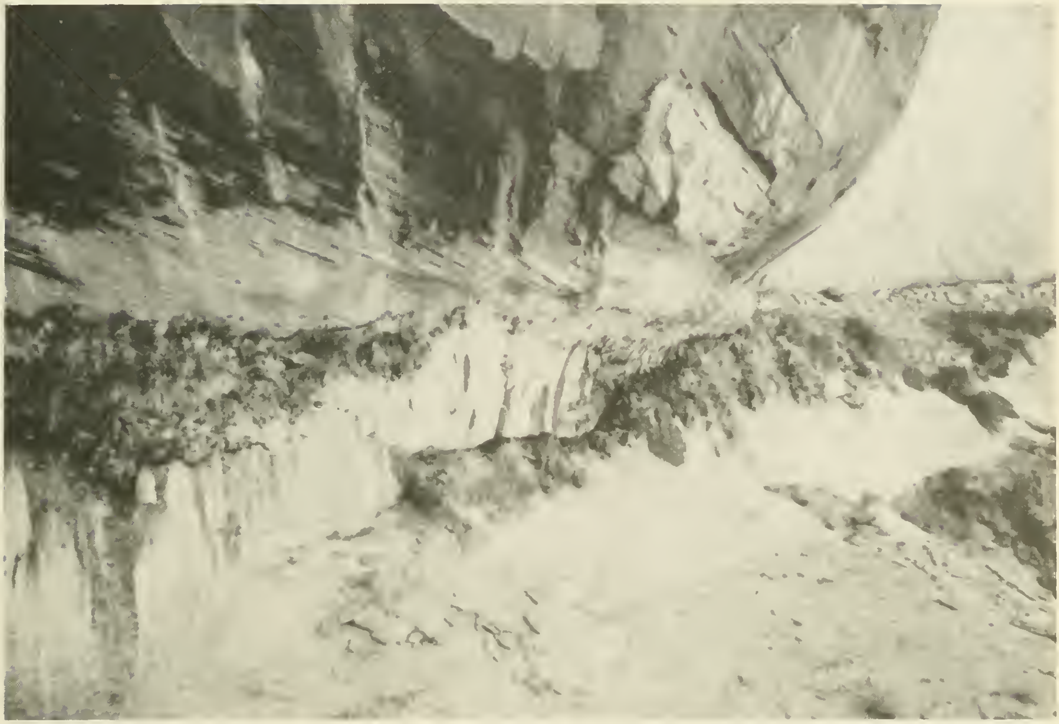

Fig. 12. Double Garden, west side of Glen Canyon, ca 1 km west-northwest of Three Garden, Kane Co., Utah. Bedding plane control of this linear garden is apparent. Hanging garden plants are restricted to the strike of the plane.

though the visitation was not adequately tested in the trapping design. Cricetids lived in all of the habitats available but reacted differently on a species-by-species basis to each habitat.

A trapability index was proposed as a device wherein the dynamics of rodent species could be partitioned within each of the habitat types. *Neotoma mexicana* and *Peromyscus boylei* showed a definite preference for the hanging garden habitat both in 1973 and 1974. *Neotoma cinerea* was indiscriminate with regard to habitat, but was not captured in the SDS during the dry year of 1974. *Peromyscus crinitus* was important in all habitat types but showed a definite preference for the SDS community. The heteromyids are habitat selective and evidently do not depend on the hanging gardens for either food or water. They are well adapted to the dry conditions in the desert plant communities external to the gardens. Although woodrats and deer mice used the gardens at all seasons, they moved from the surrounding dry habitats into the gardens during seasons of low total precipitation and corresponding low food production.

Welsh and Wood (1975) conducted productivity, cover, and composition studies on the plant community within lower Three Garden. Productivity of the gardens was high during both 1973 and 1974, even though 1974 was a dry year and productivity of the SDS community declined considerably during that year.

Similar studies of animal communities and plant productivity should be conducted in other hanging garden sites in both the Colorado and Virgin basins.

To the west, across Lake Powell from Three Garden, is Double Garden whose hanging garden vegetation is aligned along a bedding plane near the base of the Navajo Sandstone (Fig. 12).

North of Hole-in-the-Rock, where the San Juan pioneers labored so diligently, on the east side of Glen Canyon, a canyon named Ribbon enters through sentinellike monoliths of Navajo Sandstone. Immediately within the mouth of the canyon, on the south side, is a huge, perpetually shaded alcove, bearing the monument-sized Ribbon Garden (Figs. 2, 13). Within the huge alcove is a smaller one, facing westerly. Both gardens support plant

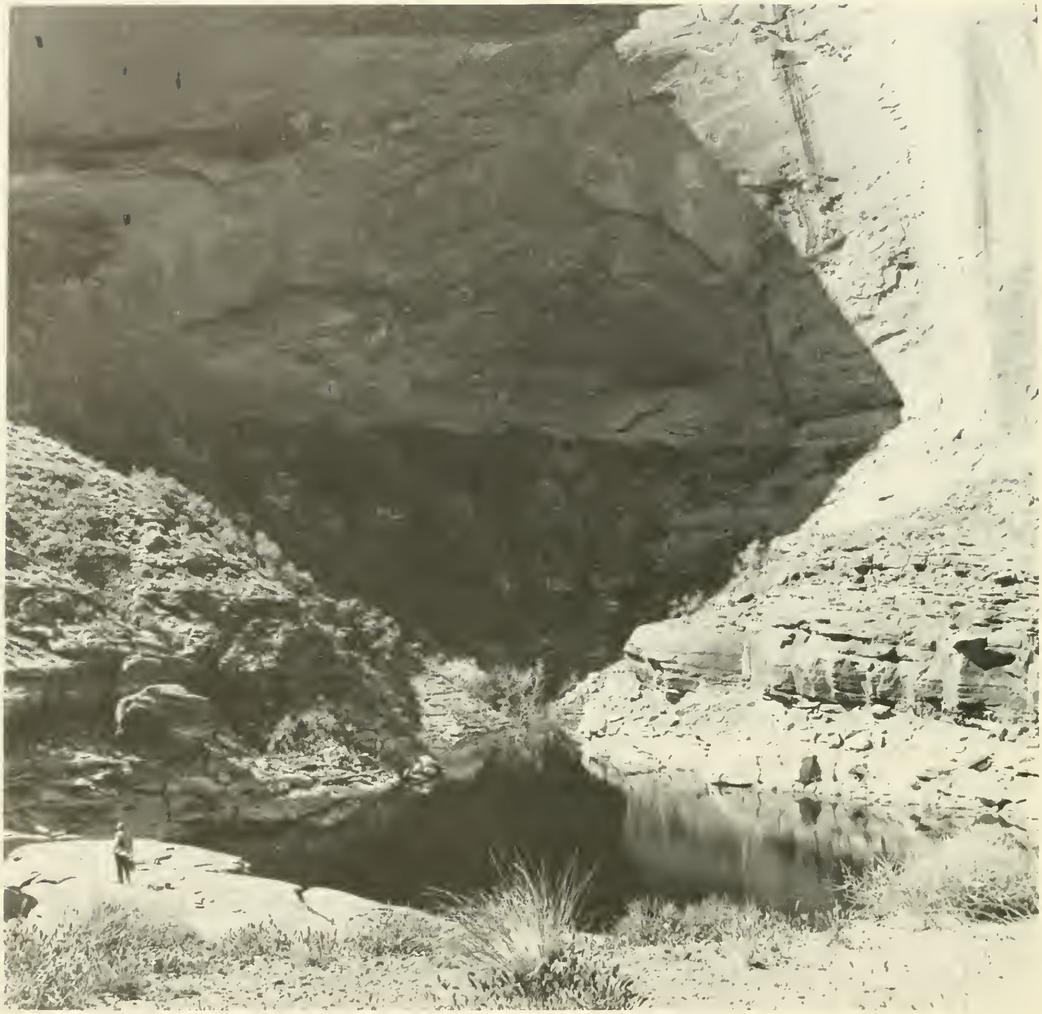

Fig. 13. Ribbon Garden, Ribbon Canyon, Lake Powell, San Juan Co., Utah. The detrital slope in the shadow is mainly on Kayenta Formation terraced margins. The slope supports a growth of New Mexico raspberry and Knowlton ironwood. A smaller alcove is present within the large alcove, which is shaded almost continuously. Its detrital slope is covered with Rydberg thistle, and small-flowered columbine clings to the wet wall.

species unusual in the Utah flora. It was here that we first discovered the New Mexico raspberry (*Rubus neomexicanus* Gray), a plant with leaves more like a currant or gooseberry and with pure white, roselike flowers to 4 cm wide. The species is known in Utah only in hanging gardens along Glen and Cataract canyons, where shaded for most of each day.

Growing with the raspberry is the Knowlton ironwood (*Ostrya knowltonii* Cov.), another rarity within the Utah flora. The small trees flower early in springtime, with staminate catkins borne pendulous from buds near branch ends. Pistillate catkins appear later, finally evident from the hoplike, inflated, papery bracts. The species is known in Utah only from along Glen Canyon and its tributaries, from the Needles section of Canyonlands National Park, and from along the Colorado River near Moab.

The small alcove on the east side of Ribbon Garden is almost perpetually in shade, and the foot slope is overgrown with a dense carpet of Rydberg thistle (*Cirsium rydbergii* Petrak), another plant confined to or near hanging gardens in the canyons of the Colorado.

The basal cluster of leaves can be up to 1 m across, much larger than any other native Utah thistle, but the flower heads are small, seldom more than 20 mm in length.

Ribbon Canyon is only a few thousand feet in length, ending abruptly in boxed ends. There are numerous alcoves along its margin, some with well-developed plunge basins. Those on the south side of the canyon support the New Mexico raspberry; those on the north do not. Water from the gardens forms a stream that flows into the lake. Reduced evaporation results in maximum stream flow at night; some of the streams and portions of hanging gardens dry completely each day in summer.

East of the mouth of Escalante Canyon, on shelfrock of Kayenta Sandstone rising gently from the water's edge on the north side of the canyon, are the Escalante gardens. There are eight alcoves carved into the base of the Navajo Formation, some of them with plunge basins. They contain the usual hanging garden species for Glen Canyon. Additionally, one of them is the type locality for the alcove daisy, *Erigeron zothecina* Welsh. Tall spires of the Toft yucca (*Yucca toftiae* Welsh) stand sentinellike along the shelfrock associated with the gardens.

Bullfrog to Hite

Near the lake end in Moki Canyon, in the first meander bend east of Halls Crossing, there is a large hanging garden along the south side of the canyon. The approach is through drowned Fremont cottonwood trees. The alcove is classic with a plunge basin, but the foot slope is brush clad, with poison ivy (*Toxicodendron rydbergii* Small) as a principal component. Poison ivy exists in many hanging gardens, but nowhere as abundantly as in this garden.

Knowles Canyon has the remnants of magnificent hanging gardens on the south side. Possibly they had plunge basins in the past, but now the lake receives the water from pour points and from the gardens. New Mexico raspberry is included in the vegetation. Garden development in alcoves on the north side is not as great, but the gardens there support an abundance of grass, with little bluestem and Jones reedgrass being common.

On the east side of the lake at Good Hope Bay there are springs surrounded by a peculiar phase of Gambel oak. The spring sites are not situated on exposed sandstone walls, but rather arise on the Chinle Formation, with water possibly developed from joint systems in the Wingate Sandstone to the east. The oak there has acorns much larger than the species elsewhere in Utah. It is called *Quercus gambelii* Nutt. var. *bonina* Welsh, the Good Hope oak. Possibly this phase of Gambel oak has been derived through hybridization and backcrossing between *Q. gambelii* and *Q. havardii* Rydb., the shinnery oak. Potentially it could exist in hanging gardens in this portion of Glen Canyon, but further exploration is necessary.

Ticaboo Canyon enters Good Hope Bay from the west. Water flows perennially down the canyon bottom for a short distance, and there is minor hanging garden development near its juncture with the lake. Here along the stream is the northernmost known locality for bushy bluestem and for the scarlet lobelia or cardinal flower (*Lobelia cardinalis* L.). The cardinal flower is known from hanging gardens in the vicinity of Gardens Cove near the San Juan confluence, and in moist situations in Zion Canyon also. Prior to the existence of Lake Powell, a peculiar species of aster was taken at Ticaboo. *Aster spinosus* Benth., the Mexican devilweed, was known from a garden in the mouth of Llewellyn Gulch, which was flooded during the high water of 1983. Otherwise the species exists as a plant of sandy and gravelly flood plains and bars north to near the confluence of the Colorado and Green rivers.

Escalante Canyon—Waterpocket Fold

Escalante Canyon was formed by entrenchment of Escalante Creek in the synclinal flexure west of the Waterpocket Fold anticline, whose east side is steeply dipping and whose west side falls more gradually to the Escalante. Two canyons near the south end of the fold drain into Glen Canyon proper. They are Bowns Canyon and Long Canyon. Bowns Canyon is of interest because of the numerous small alcoves, most of them with at least some hanging garden development. It is in this canyon that evidences of prehistoric animals, including mammoths, have been discovered amidst evidences of vegetation now confined to higher elevation, cooler portions of the state. The entrance to Long Canyon is blocked by a huge nickpoint, occupied by a moderately developed hanging garden. A

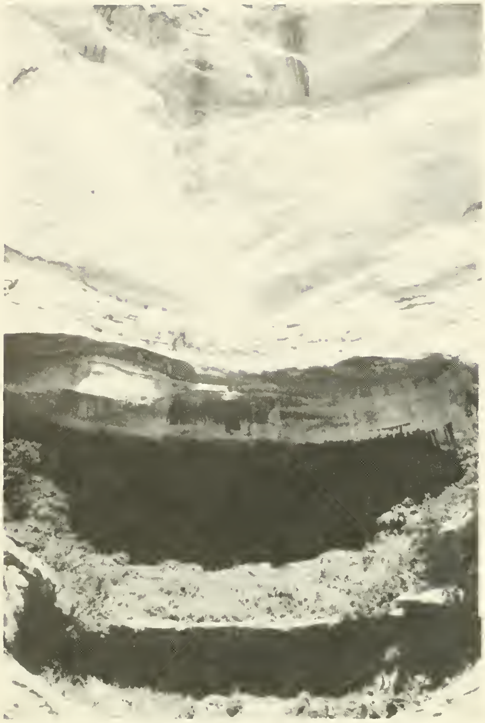

Fig. 14. Cow Canyon Garden, at the end of the Left Fork of Cow Canyon, Waterpocket Fold, Kane Co., Utah. Principal vegetation on the foot slope of the upper garden is Rydberg thistle. This is one of many alcove gardens at the base of the Navajo Formation in Cow Canyon.

route to the west will lead into the canyon, which requires additional investigation.

There are several canyons that drain west from the crest of the fold into Escalante Canyon. Explorer Canyon had a perennial stream and some garden development, but the most interesting of the Waterpocket canyons is that named Cow. Indeed, it is perhaps the most intriguing of all canyons that drain water to Lake Powell. Cow Canyon is deeply entrenched through the Navajo Sandstone into the Kayenta Formation. The slope of the canyon bottom approximates that of the dipping west slope of the Waterpocket Fold. Alcoves line the canyon walls, with one or more in each meander bend. Typically the alcoves are perched atop the Kayenta platform. The gardens often are classic alcoves with developed plunge basins, but the species complement varies with each garden—there are no two gardens alike. The canyon has two main branches, and the left-hand branch forks again near its apex. Each of the forks is terminated by box ends that form hanging gardens of huge vertical relief. The left fork terminates in paired, owl-face-like alcoves filled with greenery (Fig. 14). The right fork terminates in an alcove of great height, possibly as much as 120 m.

One alcove west of the forks of the left-hand fork of Cow Canyon is occupied by Knowlton ironwood almost to the exclusion of other woody vegetation. Other of the alcoves studied lacked this plant. Evidences of past occupation by Indians are also present. Alcoves where the bedding planes had dried support small stone structures where grain and other items derived from primitive agriculture could be stored. Dwellings are also present.

White Canyon

White Canyon drains from the west margin of Elk Ridge and enters Glen Canyon south of the Hite Marina. The canyon proper is entrenched through the Permian Cedar Mesa Formation, which consists of water-deposited sands alternating with fine-textured materials. The sands are sometimes massive, and the fine materials serve to halt the flow of percolating water. Small alcove gardens, mainly lacking plunge basins, are present in this formation. Some of the exposed aquifers are lineal, extending as strips along the exposed sandstone margin, only a few decimeters to a few meters in width. Maidenhair fern grows in these wet sites along with small-flowered columbine and the Kachina daisy (*Erigeron kachinensis* Welsh & Moore). Gardens occur here and there along much of the length of the canyon, but possibly the best of them occur within Natural Bridges National Monument, in both White and Armstrong canyons. The alcove death camas was initially collected by P. A. Rydberg and A. O. Garrett in 1911, probably from the wet spot in the canyon immediately south of Owachomo Natural Bridge. The Kachina daisy was taken from gardens on the east side of the Kachina Meander in 1963 by Welsh and Moore (1964). This plant was at first thought to be endemic to the gardens, but more recent collections show it to occur on sandy sites in ponderosa pine forests in the Abajo Mountains. It is known from hanging gardens in Dark Canyon and from along the Delores River in Colorado also.

Cataract Canyon

At the Hite Marina a buff sandstone, the Cedar Mesa Formation, is intersected by Lake Powell. This very old sandstone is a portion of the Cutler Group of formations. Slickrock margins of the lower portion of Cataract Canyon are in this formation. The slickrock supports scattered specimens of Utah juniper, narrowleaf yucca, blackbrush, and many other shrubs and grasses. The lower end of Cataract Canyon is marked by cliffs, with shelves supporting desert shrubs such as single-leaf ash (*Fraxinus anomala* Torr. ex Wats.). Redbud grows along the shelfrock also, with the vicinity of Dark Canyon marking its northern limits. Just north of Dark Canyon, on the east side of Cataract, is a poorly developed hanging garden. The garden faces north and is stained by carbonaceous black water stripes. The foot of the garden supports some of the typical garden species noted earlier. This garden is the southernmost known locality for the alcove rock-daisy, *Perityle specuicola* Welsh & Neese. It is a peculiar, rushlike member of the sunflower family with slender, drooping branchlets and small heads of cream disk flowers. The plant is known otherwise from gardens in the vicinity of Moab.

There is another poorly developed hanging garden on the south side of the first bend west of the Gypsum Canyon reentry, east of Clearwater Canyon. The garden, named Ron's Garden, is peculiar in that it is formed in limestone and has a large central pillar of tufa (similar to the tufa deposits along the trail to Zion Narrows), derived from calcium carbonate in water that has percolated through the Hermosa Formation. Besides several of the usual hanging garden plants—such as maidenhair fern, cave primrose, and the small-flowered columbine—the New Mexico raspberry is present. This is the northernmost location known for the raspberry.

San Juan Arm

At the juncture of the San Juan with Glen Canyon, the Navajo Formation rises above lake level. The canyon of the San Juan Arm of Lake Powell is entrenched in a series of meander bends, each different from the others and each with hanging gardens. On the west side of the first meander bend, almost straight through the rock less than 1 km from Three Garden, is a huge alcove, dry in its tremendous upper portion but wet along the terraced base formed from the Kayenta Sandstone. A cottonwood tree grows on the shelfrock, and a terraced type of hanging garden exists. Rydberg thistle, redbud, maidenhair fern, and alcove death camas are components of the vegetation. This is Death Camas Garden (Fig. 15). It is an excellent example of an alcove with upper bedding planes either dried or buried with detritus, but with the impervious Kayenta being wet from water percolating to its surface and flowing down its margin.

Death Camas Garden demonstrates the difference in species composition of closely spaced garden assemblages. It contains the alcove death camas, which did not occur in Three Garden, but was present in other gardens almost due west of Three Garden across Glen Canyon. The death camas occurred also in Reflection Garden. Other species show similar peculiarities of distribution.

A small canyon enters the San Juan at the north end of the first meander curve. Several hanging gardens are present in its box end and margins, in alcoves perched atop the Kayenta high above the lake surface. Most of these gardens lack plunge basins, the water having scoured the rock surface smooth and in some instances having worn swirl holes in the stone.

Nasja Canyon enters from the south in the beginning of the second meander bend. Its entry is blocked by a nickpoint in stone, whose alcove contains remnants of a depauperate hanging garden clad with small-flowered columbine, cave primrose, and a few other plant species.

Eastward along the lake, Wilson Creek enters across from Trail Canyon. The mouth of Wilson Creek is also blocked by a nickpoint, which is sometimes above and sometimes below lake level. Perennial water flows from Wilson Creek. Above the nickpoint grows a stand of saw-grass, a third known locality, if it still survives following the high lake level of 1984 and 1985. Along the stream grow cottonwood, seep willow, willow, and the beautifully plumed satintail grass (*Imperata brevifolia* Vasey), which is currently known from only this location in Utah.

Wilson Creek is evidently that described by Platte D. Lyman of the Hole-in-the-Rock expedition (Miller 1959). Lyman and party

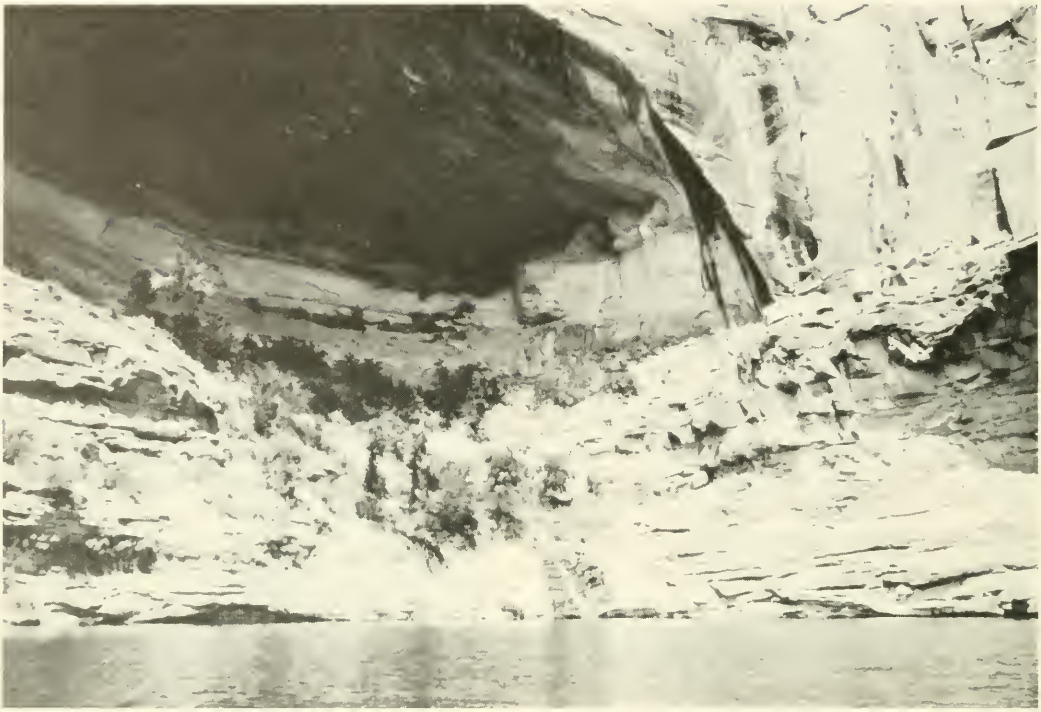

Fig. 15. Death Camas Garden, in the first meander bend east of the confluence of the San Juan and Glen Canyon arms of Lake Powell, San Juan Co., Utah. The alcove is more than 100 m wide and perhaps half as high. It supports a terrace-type garden on the bedded Kayenta Formation margin, principally Rydberg thistle, sheathed death camas, and maidenhair fern. Western redbud is prominent.

followed it down to the San Juan River. The canyon was described as having a small stream and lush vegetation. Deep water-filled holes occurred here and there, and Lyman indicated that they caught several mud turtles as large as a man's hand. These have not been found in recent times, but an occasional turtle shell has been recorded for Glen Canyon. Doubtlessly, Lyman's observation of 1 December 1879 is correct.

The Great Bend of the San Juan is marked in its outer margin by huge alcoves with hanging gardens. The alcoves are some distance from the lake. Limited investigations yielded no new distributional information from these gardens.

Bluff

Pioneer plant taxonomist Alice Eastwood (1896) took plants from the moist garden-clad alcoves near Bluff, Utah, in the 1890s. She was probably the first botanist of consequence to visit and describe the unique hanging garden habitat. She (1896) stated that the habitat "is a boreal oasis in the midst of a Sonoran desert." Gregory (1938), in speaking of the canyons of the San Juan and of Butler Wash, noted that "the spring line at the base of the bare Bluff sandstone is marked by a bank of green vegetation formed by plant species that seem out of place in the present scheme of distribution." The types of *Mimulus eastwoodiae* Rydb., *Primula specuicola* Rydb., and *Cirsium rydbergii* Petrak (*C. lactucinum* Rydb.) were collected by Rydberg and Garrett during 1911 (Rydberg 1912, 1917, Petrak 1917). *Aquilegia micrantha* Eastw. was taken from the gardens by Alfred Wetherill in 1894 (Eastwood 1896).

The Bluff Sandstone has been variously regarded, either as a member of the Entrada, a separate formation, or, more recently, as a basal member of the Morrison Formation. The stratum is not especially thick, and alcoves worn in its margin rest on the Wanakah Formation (previously regarded as Summerville).

The gardens are readily accessible in Cottonwood Canyon north of Bluff, or along the strike of the formation east or west of that canyon. The cliffs of the Bluff Sandstone are less imposing to the eastward, and the gardens are accessible at ground level. Indeed, some of the easternmost gardens are grazed by sheep and goats, who drink the water draining from them and that which accumulates in the plunge basins following storms.

The cave primrose is most impressive when in full flower, and coincidence of flowering in some years with the Easter season has led to the local common name of Easter flower. The gardens and their flowers are easily seen from the main highway through Cottonwood Canyon.

Moab and Vicinity

Examination of the plant collection in the herbarium of Brigham Young University in 1960 demonstrated the existence of *Ostrya knowltonii* Cov., represented by several sheets of a single collection taken many years earlier by Walter P. Cottam, pioneer plant ecologist at the University of Utah and prior to that professor of botany at Brigham Young University. The locality for the plant was simply "Moab." In a later discussion with Dr. Cottam I asked him from where the plant had been taken, and he replied: "I won't tell you! It is so much fun when you find it for yourself!" The collection came from a hanging garden near Moab, and I later rediscovered it there.

There are distinctive classic alcove gardens west of Moab at The Portals, east of the Colorado River bridge north of Moab, and in the reentry canyons along the Colorado River. Negro Bill Canyon has several gardens ranging in size from a few meters square to huge classic alcoves with plunge basins. The reentry canyon west of Negro Bill has a darkly shaded alcove and plunge basin at its boxed end. The garden is accessible only by considerable effort of clawing one's way through a thick growth of oak and scrambling over rock falls. Cave primrose, maidenhair fern, alcove death camas, and other species characterize these gardens. The alcove rock-daisy and alcove bog-orchid were named and typified on plants taken from alcoves in the first meander bend east of the Colorado River bridge. The gardens nearest the road are heavily impacted by humans, and they have not survived as they were when first visited by botanists following the turn of this century. Several introduced tree species have escaped and grow within or immediately in front of the gardens. Catalpa, Siberian elm, and tamarix are now growing in them. Refuse from campers and hikers clogs some of the gardens.

The Delicate Arch section of Arches National Park displays many hanging gardens. A fault line north of the trail head to that arch trends generally east-west and the Entrada Formation has an offset of some meters. The wall of that offset is marked by alcoves that continue along the strike of the formation west to Fresh Water Canyon. The trail to Delicate Arch is on the downthrown side of the fault, and the gardens are readily visible along it. Dead Tree Garden is the larger of those displayed (Figs. 16, 17, 18). It is approachable up a slickrock drainage. There is an upper alcove with a low, horizontal back wall and darkly shaded face wall. A dead juniper occupies a place on the lip of this upper alcove. Maidenhair fern and Eastwood monkey-flower grow on the back wall. The lower alcove is not so deeply cut. Its slightly indented and curved wet wall is occupied by cave primrose, magnificent in early springtime when in full flower. Alcove death camas grows along the base of the face wall and sometimes clings to the surface of the wall itself. Plants of Garber sedge and helleborine orchid hug the wall base at the back of the detrital slope. The dryish margin is clothed with little bluestem.

Island in the Sky portion of Canyonlands National Park is margined by cliffs of Wingate Sandstone. Only rarely do alcoves form in the Wingate, possibly because the capstone Kayenta is so impermeable. Exceptions to hanging garden formation in the Wingate occur at the head of Trail Canyon off the north side of the island, where a huge alcove is present in the Wingate and a small saline seep hints at a garden there in the past, and at Naturalists Cove south of the first switchback of the Schafer trail. There behind a grove of Douglas-fir and Rocky Mountain maple is a small garden supporting Fendler barberry (*Berberis fendleri* Gray), cave primrose, and Jones reedgrass. The elevation is about 1,770 m. Fendler barberry is known also from a dryish garden below The Neck.

The White Rim formation is encountered along the edge of the Green River west of

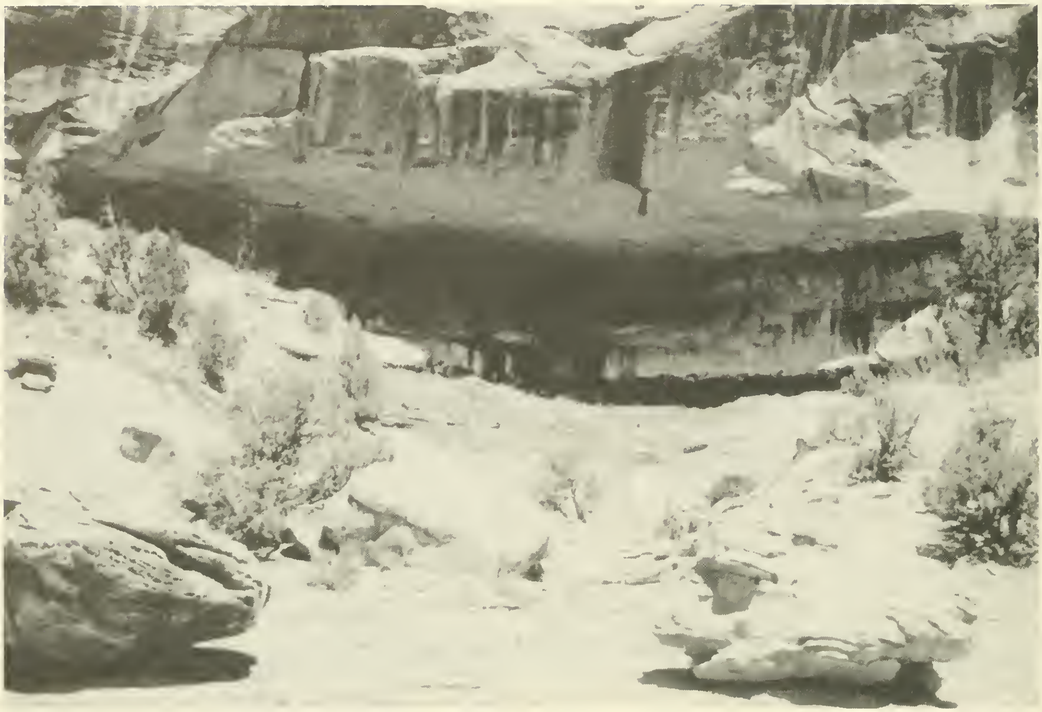

Fig. 16. Dead Tree Garden, Entrada Formation, north of the trail to Delicate Arch, Arches National Park, Grand Co., Utah. This alcove garden is controlled by a series of bedding planes in the Entrada Formation, exposed along a fault line. The upper alcove is very deep and densely shaded. Maidenhair fern clings to its flat roof.

Island in the Sky, north of Anderson Bottoms. It is best displayed downriver from Anderson Bottoms, where the formation gradually rises above the river as a prominent marginal feature. The gardens occur along its strike, with alcoves developed to the underlying impervious Cutler. The gardens have not been explored but are known to support cave primrose. More work is indicated. A poorly developed garden at Anderson Bottoms was tentatively explored as a water source by a private owner prior to establishment of the Canyonlands as a national park.

HANGING GARDEN SPECIES

Hanging garden species show diverse affinities as was outlined by Welsh and Toft (1981). Some are boreal plants, whose phenology still reflects their northern habitat regimen. Others are southwestern in their relationships, and still others have affinities with plants to the south. The following list is not meant to be exhaustive of all species that occur in the gardens. Especially listed are the plants that regularly occupy wet walls in the alcove, terrace, and windowblind gardens.

***Adiantum capillus-veneris* L.** Maidenhair fern

This plant grows in practically all hanging gardens. It occurs in the salt-encrusted gardens in the Kayenta Formation in St. George, in the gardens of Zion, and in practically all of the gardens in the Colorado drainage. Elsewhere the species is widespread. In North America it occurs from British Columbia east to South Dakota, Missouri, Florida, and Texas. It grows in much of Europe, often on calcareous tufa. The species is also present in the subtropics of both hemispheres. It fits the requirements for a hanging garden species both in being disjunct and in being the most consistent of the hanging garden wall plants.

***Adiantum pedatum* L.** Northern maidenhair fern

Northern maidenhair fern is disjunct in the hanging gardens of Zion Canyon mainly, but it occurs in some gardens in the head of the Escalante drainage of the Colorado Plateau.

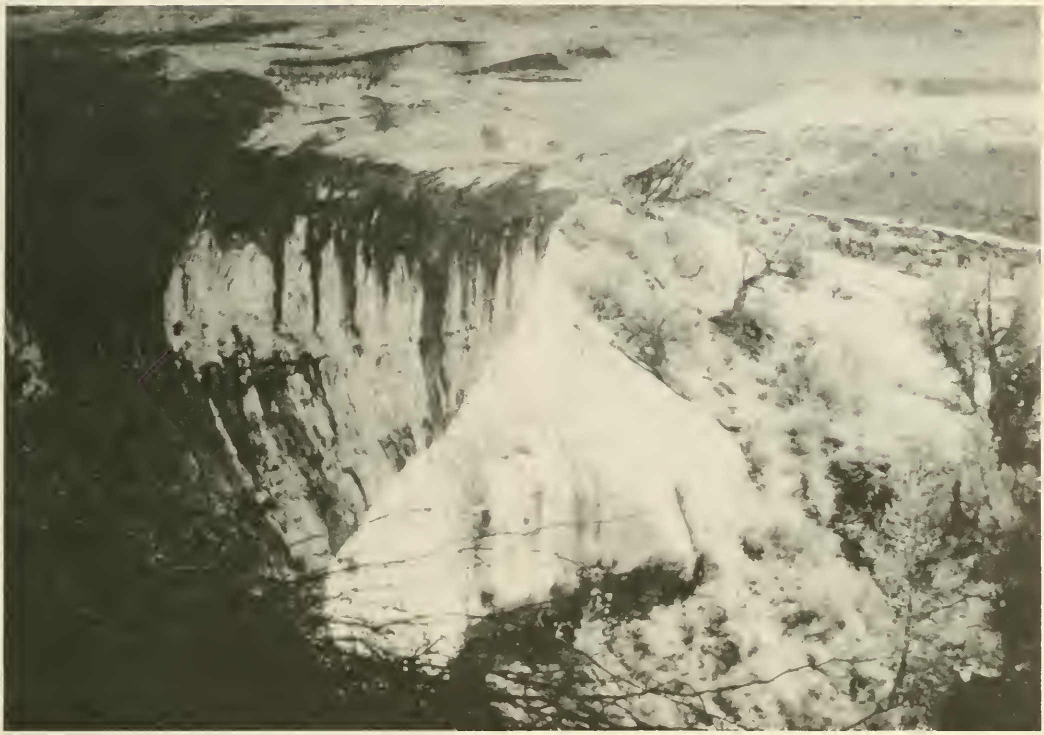

Fig 17. View east from upper alcove of Dead Tree Garden, showing clinging back and face wall plants of maidenhair fern and Eastwood monkey-flower.

Its distribution even in those areas is spotty. It grows usually beneath boulders where it is consistently more shaded than the habitats occupied by *A. capillus-veneris*. In Utah this species is not always a hanging garden plant. It grows in mesic sites in the Wasatch Mountains. The species occurs from Alaska to the Atlantic and south to California, Oklahoma, and Georgia. It is also known from Asia.

Andropogon glomeratus **(Walter) B.S.P.** Bushy bluestem

Plunge basins and detrital slopes of alcove gardens in the Glen Canyon vicinity support bushy bluestem at the northern limits of its distribution in Utah. The plants occupy a position in the gardens somewhat similar to that of saw-grass. The two plants also grow together along Furnace Creek in Death Valley, California. Bushy bluestem is a plant of warm temperate affinities through much of the southern and coastal eastern U.S. It also grows in Mexico. It is typical of a group of prairies and plains species that occur marginally to the gardens. *Sorghastrum nutans* (L.) Nash in Small, *Panicum virgatum* L., *Andropogon gerardii* Vit., and *Schizachyrium scoparium* (Michx.) Nash in Small are other examples of such species that fringe many of the hanging gardens.

Aquilegia chrysantha **Gray** Golden columbine

Golden columbine is restricted to the Zion Canyon gardens in Utah. The first flowers are very large and attractive, with spurs 4–7 cm long. It hybridizes with *A. formosa* (see below) in the gardens, and the hybrids are conspicuous and recognizable by their telltale reddish sepals and spurs. The species is known from Arizona, New Mexico, Colorado, and Mexico.

Aquilegia formosa **Fisch. in DC.** Western columbine

Zion Canyon materials of *A. formosa* are of two types. Plants of only moderately mesic crevices at 1,678 to 2,288 m elevation are glandular overall and belong to the var. *fosteri* Welsh. Seeds cascade into the canyons where some plants of that type occur in the hanging

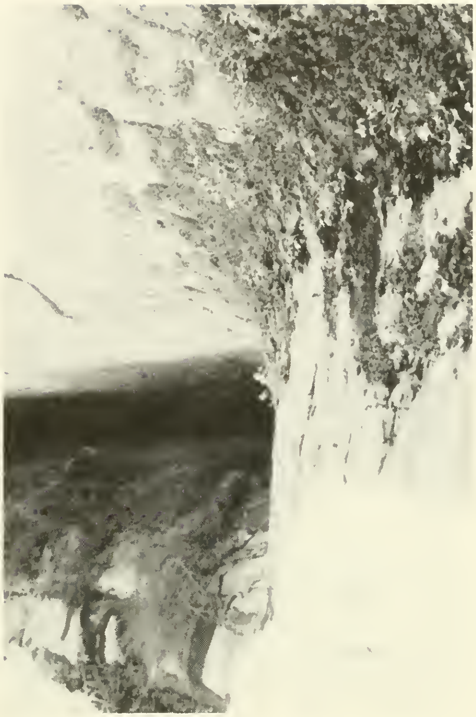

Fig. 18. Reverse view of Figure 16, showing the clinging plants on the bedding plane, whose erosion has resulted in the dark upper alcove. Etiolated plants of *Rhus aromatica* Ait. sprawl along the edge of the alcove.

gardens. There they coexist with *formosa* plants that are glandular only in the inflorescence and with *A. chrysantha*. The *formosa* type of plants that lack glandular foliage is thought to represent hybrids between var. *fosteri* and *A. chrysantha*. Their lack of glandularity on the foliage, flowers that average larger, and more mesic habitat requirements (than var. *fosteri*) suggest such an origin. Plants of the *formosa* type are known from gardens only in Zion. Elsewhere in Utah *A. formosa* grows in seeps and along streams. The species is known from Alaska and Yukon south to Baja California, Nevada, and Montana.

***Aquilegia micrantha* Eastw.** Alcove columbine

Alcove columbine is an endemic of hanging gardens of the canyons of the Colorado. It occurs in most of the gardens of that area. The small, white to cream-colored (less commonly pinkish to pale blue) flowers and overall glandularity are diagnostic for the species. Alcove columbine is not known from the Virgin River drainage. The species is known only from the Colorado Plateau of Arizona, Colorado, and Utah.

***Aralia racemosa* L.** American spikenard

This plant forms clumps that reach a height of more than 2 m and have leaves to almost 1 m wide. The umbels of small white flowers are conspicuous in early summer and are followed by rounded clusters of fruits. The plants occur primarily on the floors of grottos, where they are shaded almost constantly. Occasional plants do occur on the garden walls and in the riparian communities, especially in the Narrows. The plant is known in Utah only from Zion Canyon. The phase of the species occurring in Utah is ssp. *bicrenata* (Woot. & Standl.) Welsh & Atwood. The species occurs from southeastern Canada and northeastern U.S. southward to Arizona and New Mexico.

***Calamagrostis scopulorum* Jones** Jones reedgrass

This species was named and described on the basis of plant specimens taken from Zion Canyon by Marcus E. Jones in 1894. The species is elevationally disjunct in the hanging gardens of Utah. Its principal distribution otherwise is in boreal and alpine sites. The species occurs from Montana to Arizona and New Mexico. It is the main grass in the gardens in Zion Canyon and is often a main component of gardens along the canyons of the Colorado in eastern Utah.

***Carex aurea* Nutt.** Garber sedge; Golden sedge

The common sedge of hanging gardens in both Zion and Glen canyons vicinities differs in mainly intangible features from that typical of the species as it occurs in montane and alpine sites. It has been referred to as *C. garberi* Fern. It is usually a larger plant and has greenish rather than golden fruits of its alpine counterpart. However, it seems best to regard it as little more than an ecotype of the more broadly ranging *C. aurea*. The species is present in most of the Colorado gardens and some in Zion. It is widely distributed in North America and has been considered by some authors as a portion of the *C. bicolor* All. circumboreal complex.

***Carex curatorum* Stacey** Canyonlands sedge

This primocarex is easily recognized by its solitary, unisexual spikes borne on separate plants. The species is elevationally disjunct in the gardens of the Colorado canyons from the confluence of the San Juan with Glen Canyon to the head of the Escalante drainage. Occasional specimens have been taken at high elevations as far north as central Utah. The species has recently been detected in Zion Canyon. Otherwise the species is known only from Arizona. Its affinities are with the boreal *C. scirpoidea* Michx., with which it has been combined at varietal rank.

***Cercis occidentalis* Torr. ex Gray** Western redbud

This beautiful plant produces masses of red-pink flowers in early springtime. It is a regular occupant of hanging gardens in Glen Canyon, where it also occurs as a crevice plant not associated with hanging gardens. The species is present as far north as the mouth of Dark Canyon, a tributary of Cataract Canyon, where it grows on sandstone outcrops on the shaded side of the canyon. In the Virgin River drainage the species does not occur in hanging gardens. Rather, it occupies moist north-facing sites in sandstone along the Santa Clara River and shaded, dryish alcoves in limestone in the Beaver Dam Mountains. In hanging gardens the plants sometimes grow attached to the face wall, but more often they grow on the moist ledges at the base of the detrital slope, where they are typically associated with *Celtis reticulata* Torr., *Quercus gambelii* Nutt., and *Q.* x *eastwoodiae* Rydb. Affinities of this redbud lie with *Cercis canadensis* L., a species of eastern American summer deciduous forest affinities, with which it is sometimes combined at varietal rank.

***Cirsium rydbergii* Petrak** Rydberg thistle

The Rydberg thistle is an endemic of hanging gardens in the canyons of the Colorado. Rarely it occurs outside the gardens along drainages. It is a perennial, with huge basal rosettes sometimes more than 1 m across. The flower heads are small, however. It does not occur in Virgin River drainage gardens and has no counterpart. *Cirsium virginensis* Welsh grows in the gardens in St. George but is principally a riparian species. The same is true for *C. calcareum* (Jones) Petrak, which grows in some of the hanging gardens in the Colorado Plateau proper.

***Cladium californicum* (Wats.) O'Neill in Tidestr.** Saw-grass

This plant reached its northern distribution in hanging gardens along Glen Canyon. It was collected historically at the mouth of Kane Creek, now under several hundred feet of water held back by Glen Canyon Dam. Subsequent collections were taken at Step Garden in Driftwood Canyon, Cladium Garden in Hidden Passage Canyon, and Wilson Creek along the San Juan Arm. The high water of 1983 and 1984 lapped at the margin of the great clump of this species at Step Garden and apparently drowned a portion of the plants at the mouth of Wilson Creek. Cladium Garden has long since been inundated. A second small patch of saw-grass is present at the foot of one of the vertical walls in Hidden Passage Canyon, however. The plant is precariously situated in the flora of the region. Elsewhere it is known from along Furnace Creek in Death Valley, California, and when considered as a portion of the broadly distributed *C. mariscus*, its distribution is across much of the southern U.S. and southward.

***Dodecatheon pulchellum* (Raf.) Merrill** Pretty shooting-star

The Zion Canyon phase [var. *zionense* (Eastw.) Welsh] of the shooting-star is also known from hanging gardens in Little Valley tributary of Last Chance Creek, north of Lake Powell, in the Escalante drainage, and along Lake Powell as far north as the confluence of the Escalante. Nowhere does it grow so profusely as in the shaded gardens of Zion Canyon. The species occurs in much of Utah and is widely distributed in western North America and disjunctly in the eastern U.S.

***Epipactis gigantea* Dougl. ex Hook.** Helleborine

This plant is mainly palustrine in its distribution, occurring around seeps and springs and along streams in much of western North America from the Canadian provinces southward. It is a common component of the alcove hanging gardens in southeastern Utah. The purplish to greenish purple or purple-brown flowers are displayed on plants that are usual at the juncture of detrital slopes and adjacent face walls in many gardens. It grows there with Garber sedge, bundle panic, and other garden species. The plant is not especially noted as a garden species in Zion Canyon, however. It is in the canyon but occupies marshy sites in The Narrows, where garden development is not especially prominent. A single clump of the plant is present in a dryish garden associated with maidenhair fern along the trail to Refrigerator Canyon in Zion Canyon.

***Erigeron kachensis* Welsh & Moore** Kachina daisy

This pretty dwarf daisy produces stolons that allow it to grow on wet walls and moist sand in hanging gardens in Natural Bridges National Monument and Dark Canyon, Utah, and along the Dolores River in Colorado. The plants also occur as mere mesophytes in other plant communities besides hanging gardens at higher elevations in the Abajo Mountains. It is a Colorado Plateau endemic.

***Erigeron sionis* Cronq.** Zion daisy

The Zion daisy is a stoloniferous mesophyte. The stolons tend to bind the plant in colonies on moist sandstone. The nature of the stone in Zion Canyon allows water to percolate in shallow stone lenses, only to come to the surface along minor defiles. Some of the moist lenses are hand-sized and still support this daisy. The plants are provided with water for some time following snow melt in springtime or following rains at any season. Hanging gardens also serve as habitat for this plant, which is especially common along minor terrace margins and on rock faces in the grotto floors. Occasionally the plants grow along drainages below the gardens, and rarely the plants are found growing well on apparently dry sand. The plant is endemic to Zion Canyon.

***Erigeron zothecinus* Welsh** Alcove daisy

Alcove daisy is known only from a suite of hanging gardens (the North Escalante Gardens) on the north side of Glen Canyon immediately east of the confluence of the Escalante Canyon. It is confined to the wet walls and foot slopes of small gardens near the base of the Navajo Sandstone or top of the Kayenta Formation. The eight main alcoves in the Navajo to the north apparently do not support this plant.

***Habenaria zothecina* Higgins & Welsh** Alcove bog-orchid

Long thought to be a phase of *H. sparsiflora* Wats., this species with long-spurred flowers was named from the hanging gardens of the first meander bend east of the Colorado bridge north of Moab, Grand County, Utah. The species occurs in hanging gardens from Arch Canyon, west of Comb Reef, north to Arches National Park. It is endemic to the hanging gardens.

***Lobelia cardinalis* L.** Scarlet lobelia

This third of a triumvirate of plants with scarlet or brilliant red flowers is less likely to occur within the garden flora than adjacent to it. The species is rather common on the wet walls of Zion Canyon, however. The other two, *Mimulus cardinalis* Dougl. ex Benth. and *Mimulus eastwoodiae* Rydb., are characteristic of the gardens proper, even though they also occur on the downslope portions of the garden and less commonly along the drainages below them also. Those downslope and down drainage localities are the common sites occupied by scarlet lobelia in the Colorado canyons gardens especially. The species is present in Zion Canyon and along Glen Canyon as far north as the mouth of Ticaboo Canyon. It is widely distributed in the eastern United States, Mexico, and Central America.

***Mimulus cardinalis* Dougl. ex Benth.** Cardinal monkey-flower

This plant with brightly colored, large flowers reaches the northern limits of its distribution in the hanging gardens of Zion Canyon. Its entire distribution otherwise is in New Mexico, Arizona, Nevada, California, Oregon, and Mexico (including Baja California). Utah materials have sometimes been treated as a separate species, *M. verbenaceus* Kearney & Peebles, but the ranges, when treated separately, overlap and the characters used as diagnostic fail individually and in tandem. The plants are common in the gardens of Zion where they occur both as wall and floor plants in the grotto and windowblind gardens.

***Mimulus eastwoodiae* Rydb.** Eastwood monkey-flower

Back and face walls are the common sites of placement for this species in the alcove gardens of the canyons of the Colorado. The species is in most of the gardens where it shares the walls with cave primrose. It is a smaller plant in all respects than is the cardinal monkey-flower. Flowers are borne in late summer and autumn in this species. Its counterpart in Zion Canyon is mainly a spring-flowering plant, but flowering continues through the summer. The species is endemic to the hanging gardens.

Panicum acuminatum **Swartz** Bundle panic

Gardens of the Colorado canyons typically support this plant, growing intermixed with Garber sedge on the detrital slopes of alcoves. It is less common in Zion Canyon. This is a Dicanthelium panicum, which has broad basal leaves. Flowers of two types are produced, open pollinated flowers at the summit of the plant and flowers that remain in the enclosing sheath that are self-pollinated. The species has passed under several names. It is a widespread plant in the U.S., portions of Canada, and Mexico.

Perityle specuicola **Welsh & Neese** Alcove rock-daisy

Type locality for this species is the alcove immediately adjacent to the highway on the first meander bend east of the Colorado River bridge north of Moab. The plant grows there, hanging from crevices in the back wall of the alcove. It simulates *Stephanomeria tenuifolia* (Torr.) Hall with which it grows in both habit and position. The plants also grow in the hanging garden on the west side of the same meander bend, but there on the dry edge of the garden the plants stand erect. A second population is known from a small garden in Cataract Canyon north of its confluence with Dark Canyon. The plant is not otherwise known.

Petrophytum caespitosum **(Nutt.) Rydb.** Rock spiraea

Rock spiraea grows in hanging gardens both in Zion and along the canyons of the Colorado. It does well in some of the alcove gardens where the substrate is wet, even growing associated with the algal mat on the walls, but is common in gardens that are dry. In Zion Canyon it is mainly a plant of garden margins. Often the plants occur as mats conforming to the contour of the surface, but sometimes the plant swings away from the wall and hangs pendulously from the overhanging back of alcove gardens. Spikes of creamy flowers are borne in late summer and autumn. The species grows elsewhere on limestone and igneous outcrops, typically at middle elevations, from Washington to South Dakota and south to California, Arizona, New Mexico, and Texas.

Primula specuicola **Rydb.** Cave primrose; Easter flower

The cave primrose was evidently first collected by Alice Eastwood in 1895 in the alcove gardens at Bluff, Utah. She mistakenly identified the plants with an Old World member of the genus but recognized the unique nature of the gardens and the misplaced distributions. The species might be regarded as the botanical motif of Canyonlands hanging gardens, but that role is shared practically always with Eastwood monkey-flower and small-flowered columbine. The flowers vary in color from pink (the usual color) to lavender, maroon, and white. Rarely the inflorescences are superposed as in some cultivated species, and rarely too the flowers are double. The plant is a hanging garden endemic.

Smilacina stellata **(L.) Desf.** Solomonseal

Widespread in much of North America from the subarctic southward, this species is a common mesophyte. It grows in moist sites throughout Utah, not surprisingly in hanging gardens. The hanging gardens are elevationally placed below the general distribution of the species, and thus the species seems to be a somewhat regular occupant. Solomonseal occurs in gardens in Zion and Glen canyons, mainly on the foot slope or downward along the drainages.

Solidago sparsiflora **Gray** Alcove goldenrod

Gardens of the Canyonlands region of eastern Utah are practically always partially clothed with alcove goldenrod. It is a plant of face walls and detrital slopes. Stream courses below hanging gardens and sometimes the gardens themselves also support specimens of *S. canadensis* L. Intermediates are known between these species, and some garden plants are difficult to assign to one or the other of them. The plant is less often a component of Zion Canyon gardens. Nevada goldenrod, *S. spectabilis* (D.C. Eaton) Gray, grows in the hanging gardens in St. George. Elsewhere it is a palustrine or riparian species. Alcove goldenrod is a common species, especially at elevations far above that typical for hanging gardens, in the western U.S., from Wyoming and South Dakota south to Arizona and Nevada.

Zigadenus vaginatus **(Rydb.) Macbr.** Sheathed death camas

This death camas occurs sporadically in the hanging gardens of the canyons of the Colorado. Pool Garden in Reflection Canyon, Double Gardens on the west side of Glen Canyon, Three Garden, and Death Camas

Garden in the first meander bend of the San Juan east of the confluence with Glen Canyon were essentially aligned and distant directly not more than 3–4 km. Sheathed death camas was in Pool Garden, Double Garden, and Death Camas Garden, but not in Three Garden. This hit-and-miss distribution was characteristic of the large alcove gardens along Glen and San Juan arms. The plants occur in hanging gardens north to Arches and in seëps evidently north to Dinosaur National Monument. Relationships of this species lie to the south with *Z. volcanicus* Benth. of Central America. The type of *Anticlea vaginata* Rydb. (Rydberg 1912) was taken at Natural Bridges National Monument, probably in the seep beneath Owachomo Bridge.

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CHANGES IN MULE DEER SIZE IN UTAH[1]

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ABSTRACT.—Trends in age-specific, eviscerated carcass weights were determined for hunter-harvested yearling and two-year-old buck mule deer. Carcass weights declined over an 11-year period from two areas of similar management, but with independently collected data sets. Carcass weights also declined between the opening and second weekends of the hunt. Management implications are discussed.

Mule deer (*Odocoileus hemionus*) bucks, especially large, mature animals, have sport hunting, economic, and intrinsic values (Wennergren 1968). However, perceptions of a quality hunt or buck vary considerably among hunters as evidenced by the various types of hunts established by state wildlife agencies in response to hunter input. As hunting intensity has augmented and increased the impacts on wildlife populations, and as human population growth has usurped range areas traditionally used by wildlife, game managers have been increasingly pressed to maintain quality programs. Consequently, in Utah either-sex hunting regulations during the 1960s were replaced by buck-only restrictions in the early 1970s to compensate for increasing hunter numbers using a limited resource. Antler restriction and limited-entry hunts have become increasingly common in the 1980s, with motivation for more restrictive regulations coming from hunters and biologists interested in quality hunting in terms of maintaining high numbers of mature, harvestable bucks, and restricting hunter numbers. This paper examines long-term trends of age-specific changes in the size of hunter-harvested mule deer in Utah.

METHODS

STUDY AREAS.—The Daniels Canyon checking station located in north central Utah stopped about 17,000 hunters per year (1975–85), with about 70% of the hunters returning from the Current Creek and Avintaquin deer units. The Blacksmith Fork station in northern Utah checked about 2,700 hunters (1973–83) from a portion of the Cache deer unit, mostly within the Blacksmith Fork drainage. Between 1973 and 1985 both areas had 11-day buck-only hunts, except in 1973 when the area served by the Daniels Canyon station held a three-day either-sex hunt followed by eight days of buck-only hunting. All deer hunts began the Saturday closest to 20 October.

DATA COLLECTION.—Checking station data were collected and reviewed for the two areas. Eviscerated carcass weight, age, and antler tine data were collected at checking stations during most years. Data were collected during the first and/or second weekends of the hunt. Deer were weighed to the nearest .5 kg and field aged as 1¹/₃, 2¹/₃, or 3¹/₃+ years by tooth eruption and wear methodology (Robinette et al. 1957). All antler tines exceeding 2.5 cm (Robinette et al. 1977), but excluding brow tines, were counted on intact antler pairs only at Daniels Canyon.

DATA ANALYSES.—The factors of year, age class, and weekend were initially used for analyzing the carcass weight data (1975–85) from Daniels Canyon. However, because there were many missing three-way cells, and there appeared to be a significant difference between weekends, the data were divided into four sets for analysis: (1) first week, age 1, (2) first week, age 2, (3) second week, age 1, and (4) second week, age 2. Least squares procedures and a two-factor linear model were

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[1] This paper is, in part, a contribution of Utah State Division of Wildlife Resources, Federal Aid Project W-105-R.
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TABLE 1. Deer carcass weights and tine counts from Daniels Canyon and Blacksmith Fork checking stations, Utah (sample sizes in parentheses).

	First weekend		Second weekend			
Age (in years)	1⅓	2⅓	1⅓	2⅓	1⅓	2⅓
Year	Weight[1]	Weight	Weight	Weight	Tines[2,3]	Tines[4]
Daniels Canyon						
67–68	44.9 (19)	57.2 (14)	—	—	—	—
75	45.1 (85)	58.3 (29)	43.7 (42)	56.1 (10)	16.5 (127)	17.9 (39)
76	44.0 (140)	58.5 (38)	43.1 (95)	55.5 (24)	—	—
77	43.8 (38)	59.5 (9)	—	—	—	—
78	42.5 (46)	52.7 (7)	—	—	—	—
79	—	—	41.9 (50)	55.7 (27)	—	—
80	—	—	41.0 (52)	50.6 (2)	44.2 (52)	50.0 (2)
81	—	—	40.6 (104)	51.8 (5)	26.0 (104)	20.0 (5)
82	—	—	42.1 (82)	53.4 (7)	18.3 (82)	57.1 (7)
85	41.1 (59)	52.3 (6)	40.6 (53)	51.9 (10)	33.0 (273)	27.2 (33)
87	41.1 (51)	54.1 (53)	—	—	26.8 (1627)	30.2 (69)
Blacksmith Fork						
66	47.2 (33)	63.9 (12)				
73	50.1 (22)	64.8 (11)				
79	44.2 (44)	58.9 (14)				
80	43.0 (45)	60.6 (6)				
81	41.9 (40)	No Data				
83	41.6 (43)	56.7 (6)				
86	44.4 (52)	No Data				
87	42.8 (102)	54.5 (32)				

[1] Eviscerated carcass weight (kg).

[2] A tine is defined as a minimum length of 2.5 cm excluding brow tines.

[3] Percentage of yearling deer with two tines on both antlers combined (spikes).

[4] Percentage of 2⅓-year-old bucks with four or fewer tines on both antlers combined.

used. Deer aged 3⅓+ years were not considered in this manuscript because of the potential variation of actual age within the class. The data from Blacksmith Fork (1973–83) were consistently collected on the first weekend. These data were independently analyzed using the same statistical test as a check to the conclusions of the Daniels Canyon analysis.

Antler data from Daniels Canyon were analyzed using chi-square comparisons of tine counts across years. Because the weekend effect was not significant, the data were pooled.

Because of the important implications derived from the data sets, additional, supplementary data were obtained. Two sets of carcass weight data, collected before 1970, but under either-sex hunting regulations, were compared using the 95% confidence intervals to the endpoints of the regression equations. Three sets of recent data were collected after 1985 for data trend verification and were similarly compared.

RESULTS

Carcass weights from Daniels Canyon decreased ($P = .02$) between the first and second weekends. Yearling bucks decreased a mean 2.1% in weight, and two-year-old bucks declined 3.3% between weekends.

Over an 11-year period, trends in carcass weight have been negative at Daniels Canyon (Fig. 1). Between 1975 and 1985 the weight of yearling bucks decreased 8.9% ($P = .03$) and 7.1% ($P = .02$) for the first and second weekends, respectively. Weight in two-year-old bucks decreased 10.1% ($P = .12$) and 7.5% ($P = .03$) for weekends one and two, respectively.

Results of the Blacksmith Fork analysis during a comparable period (1973–83) showed a similar decrease in carcass weight. Weight in yearlings declined 17.0% ($P = .005$) and 12.5% ($P = .04$) in two-year-old bucks.

Tine counts of yearling bucks checked at Daniels Canyon (Table 1) were greater in 1975 than during 1980–85 ($P = .01$). In 1975, 16.5% of the harvested yearling bucks were spikes, whereas the mean percentage of spikes harvested 1980–85 was 30.4%, with three of four years being significantly different

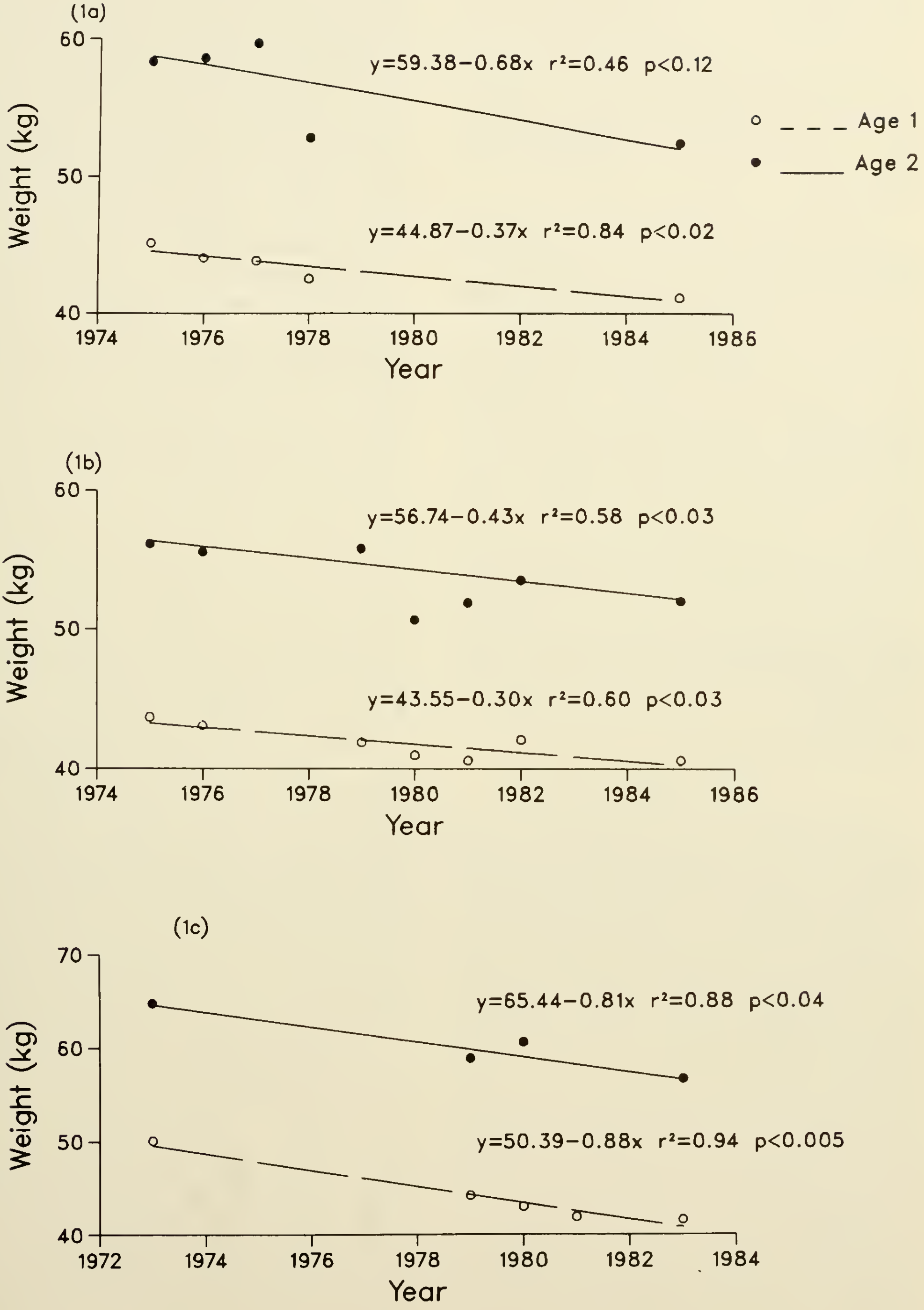

Fig. 1. Decline of mean eviscerated weight of hunter-harvested buck deer aged $1^1/_3$ and $2^1/_3$ years during the first (1a) and second (1b) weekends of the regular Utah deer hunt from Daniels Canyon checking station and during the first weekend from Blacksmith Fork (1c).

from 1975 ($P = .05$). However, significant differences were also found among years from 1980 to 1985 ($P = .01$). Tine counts of two-year-old bucks at Daniels Canyon in 1975 did not differ from combined years 1980–85 ($P = .21$) or among years 1980–85 ($P = .26$). However, 17.9% of bucks in 1975 had four or fewer antler tines, whereas in 1980–85, the mean was 31.9%.

Data collected at Daniels Canyon 1967–68 were combined because of small sample sizes (Table 1). The mean weights for yearling and two-year-old bucks (1967–68) were not different from the 1975 predicted weights. Yearling weights were different from the 1985 value, but two-year-old buck weights were not different. Both yearling and two-year-old buck weights from Daniels Canyon (1987) were not different from the 1985 predicted weights, but were different from those of 1975. Weight data from Blacksmith Fork (1966) were not different from the 1973 weights, but differed from the 1983 weights. The 1986 yearling weights differed from both the 1973 and 1983 predicted weights. Weights for both yearlings and two-year-old bucks in 1987 did not differ from those of 1983, but did differ from the 1973 weights.

DISCUSSION

The decrease in carcass weight between the first and second weekends of the hunt indicates the need for consistent timing of data collection. The data also suggest that physical condition indices (e.g., Austin 1984) collected during the first weekend of the hunt would not be representative of the herd at the hunt's end. A probable cause of the weight loss between weekends is hunter harassment, although other factors, including rutting activity and hunter selection, may also be important. Nonetheless, where overwinter survival is questionable, this degree of weight loss may be important, particularly its impacts on does and fawns.

Reduction in carcass weight and the corresponding, although weaker, reduction in number of antler tines suggest that age-specific deer size has declined in Utah. In our study, and others, weight appears to be the more sensitive index (Kie et al. 1983, Williams and Harmel 1984). Results from Daniels Canyon and Blacksmith Fork show a gradual decline in buck size from the same deer populations over more than a decade. Both areas were under similar management and showed about the same loss in size of deer.

Data collected since 1985 at both Daniels Canyon and Blacksmith Fork supported the findings of reduction in body size, in that mean weights and numbers of antler tines remained low. Data collected previous to 1970 suggest age-specific deer size probably did not decrease before the early 1970s.

A probable consequence of size decline in younger age classes is a parallel reduction in age-specific size of mature bucks. Williams and Harmel (1984) reported changes in number of antler points and live-body weights of 60 pen-reared white-tailed buck deer, fed 16% protein diet *ad libitum*, during ages $1\frac{1}{2}$, $2\frac{1}{2}$, and $3\frac{1}{2}$ years. They found that the number of antler points and the weights at ages $2\frac{1}{2}$ and $3\frac{1}{2}$ years were directly correlated with the number of antler points and weights attained by the same deer at younger ages. The corollary is that weight and antler size of older-aged bucks are also related to yearling characteristics. Consequently, the probability of older bucks being large trophy has likely also declined in Utah.

Regulations of Utah's deer hunt changed from either-sex to buck-only hunts in the 1970s, with 1973–74 being transition years. Because data collected prior to 1970 suggested no age-specific changes in size, attention should be given the potential effects of changing regulations and their effect on buck populations and quality of animals. However, partitioning the important factors potentially responsible for the observed decline was not possible. Nonetheless, several factors should be considered. First, phenotypic changes in deer populations due to hunter selectivity for larger bucks may have occurred. Scribner et al. (1984) demonstrated through modeling that selective removal of spike white-tailed bucks will gradually lower the incidence of spikes in the buck population; conversely, selective removal of nonspike yearlings would increase the incidence of spikes. Second, with increasingly wide buck-to-doe ratios and the lowering of the mean age of the buck population, both of which result from intensive buck-only hunting, a delay in the mean breeding date causing a similar delay in the fawning date may have occurred. In support, Reimers

(1983) showed a significant relationship between a delay in the date of calving and reduced dressed weight of females 2+ years in wild reindeer (*Rangifer*). Third, a density-dependent response to buck-only hunts may have occurred. Buck-only regulations may have allowed population density of females and fawns to increase and, consequently, nutrition limited phenotypic expression of genetic potential. In support, the modest rebound in weight from Blacksmith Fork in 1986 followed a marked population decline due to previously harsh winters (1983–85). McCullough (1979) discussed population growth within finite available resources and demonstrated a decrease in recruitment as carrying capacity was approached. A similar decrease apparently occurs in animal size, as observed for yeld hinds (Clutton-Brock and Albon 1983). Kie et al. (1983) reported reduced body weights and number of antler tines with increased density of white-tailed deer. Finally, climate has been shown to affect fluctuations in deer size on a yearly basis (Robinette et al. 1977), and, consequently, long-term weather trends might also be involved. Additional research is needed to identify the specific factors involved, as well as management alternatives to address the problem.

In summary, eviscerated carcass weight and number of antler tines for yearling and two-year-old buck deer were shown to decrease from 1973 to 1985 in two areas of Utah under buck-only hunting regulations. Although the reduction in size corresponded with changes to buck-only hunting, the effects of individual factors could not be partitioned.

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WHITE-TAILED PRAIRIE DOG (*CYNOMYS LEUCURUS* MERRIAM) DIGGINGS IN WESTERN HARVESTER ANT, *POGONOMYRMEX OCCIDENTALIS* (CRESSON), MOUNDS

William H. Clark[1] and Cynthia J. Clark[1]

ABSTRACT.—We report observations of the white-tailed prairie dog, *Cynomys leucurus* Merriam, digging and burrowing into mounds of the western harvester ant, *Pogonomyrmex occidentalis* (Cresson), in Emery County, Utah.

On 16 July 1987 we observed evidence of white-tailed prairie dog (*Cynomys leucurus* Merriam) digging into the mounds of *Pogonomyrmex occidentalis* (Cresson) near Wellington, Emery County, Utah. We observed two white-tailed prairie dogs sitting on the edge of a *P. occidentalis* mound at 1630 hr. Investigation of the ant nest revealed an active prairie dog entrance at the base of the mound and 12 large exploratory holes dug into the mound (Fig. 1). The entrance (11 cm diameter) was actively used, with numerous tracks, scats, and bits of vegetation adjacent to it. The burrow angled downward to the southeast and went directly under the ant mound and presumably through the center of the ant nest. The exploratory holes dug into the ant nest averaged 10 cm diameter and 15 cm deep. Of 20 ant mounds surveyed in the immediate area, 55% had the large exploratory holes;

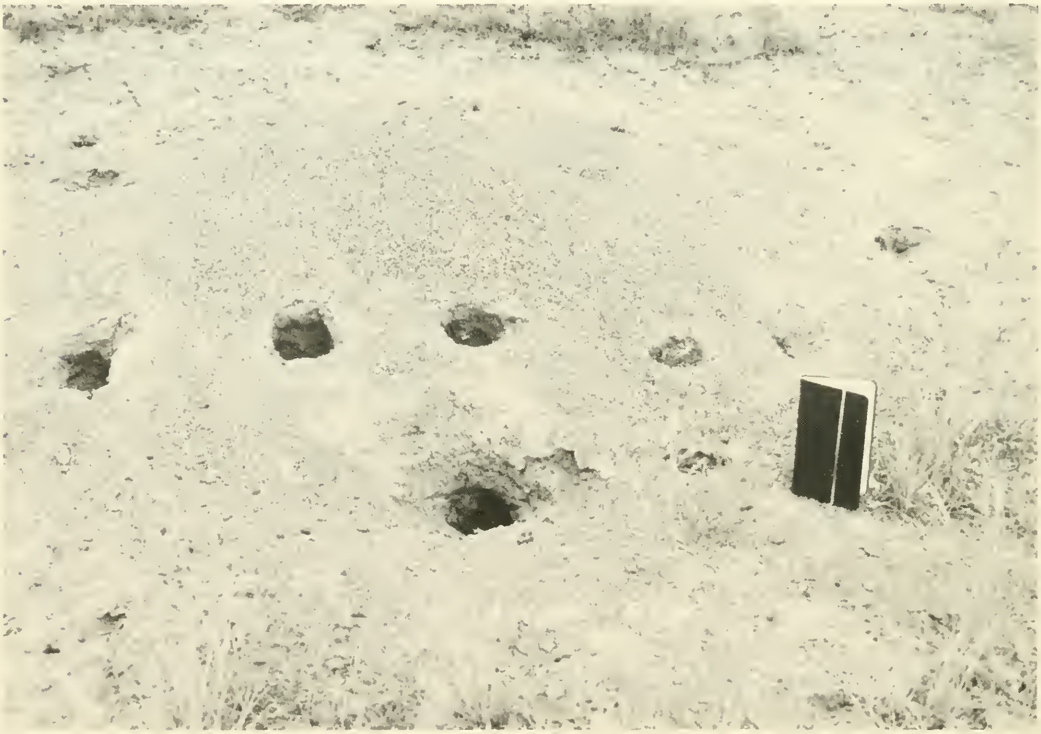

Fig. 1. Mound of *Pogonomyrmex occidentalis* showing prairie dog burrow entrance and exploratory diggings. Prairie dog droppings can be seen in the lower portion of the photo. Scale: the field book is 11 × 19 cm.

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however, holes were not found in the adjacent ant clearings or nearby vegetated areas. Thus, the mounds appeared to be selected as exploratory digging sites. Effects of the digging on the ants are not known.

Clark and Comanor (1973, Occ. Pap. Biol. Soc. NV 34: 1–6) reported heteromyid rodent digging activity into mounds of *P. occidentalis* in Nevada and Utah apparently to obtain seeds stored by the ants. Allred (1982, Great Basin Nat. 42: 415–511) made many collections from *P. occidentalis* nests in Utah but reported only one mound with two rodent burrows. Little else has been reported in the literature concerning the use of these ant mounds by small mammals.

ACKNOWLEDGMENTS

Mary and Karen Clark assisted with the field observations. Eric Yensen reviewed the manuscript and offered valuable suggestions. Voucher specimens of the ants (WHC #8187) were deposited in the Orma J. Smith Museum of Natural History, College of Idaho, Caldwell (CIDA).

AMPHIBIANS OF WESTERN CHIHUAHUA

Wilmer W. Tanner[1]

ABSTRACT.—This third report on the herpetofauna of Chihuahua deals exclusively with amphibians. The first plethodonid salamander is reported, the species *Ambystoma rosaceum* is discussed in greater detail than before, and two subspecies are recognized. *Spea* is elevated from subgeneric to generic rank, and *S. stagnalis* Cope is removed from synonymy and is recognized as a subspecies of *hammondii*. The species listed include the following: 2 salamanders and 19 anurans (1 *Scaphiopus*, 2 *Spea*, 9 *Bufo*, 1 *Eleutherodactylus*, 2 *Hyla*, 3 *Rana*, and 1 *Microhyla*).

Reference is made to various habitats that are associated with elevations arising from lower deserts and extending into the western mountains. The role played by the dry and wet annual cycles is also noted.

This is the third report on the herpetology of western Chihuahua (Tanner 1985 [1986], 1987). It deals only with the amphibians. As indicated in the preceding reports, the state of Chihuahua is a large area and includes deserts on the east, steppe foothills and valleys in the central part (north to south), and the north end of the Sierra Madre Occidental in the west. This diverse geographical terrain provides numerous and multiform types of habitat.

One wishing to gain a general understanding of the terrain of southern and northwestern Chihuahua would benefit by reading the account by Goldman (1951), which deals with the explorations of Nelson and Goldman during the late 1890s. Although their activities did not include exploration of the entire state, they did include considerable travel in northern Chihuahua extending into the deserts, mountains, and valleys and to the northeast and west of Casas Grandes. The trip by Goldman from Parral to Batopilas is replete with descriptions of this extensive area. The central area west from Ciudad Chihuahua to Madera and southwest to the extensive areas north and west of Creel were not explored.

Although these exploratory field trips provided valuable information concerning the general nature of the terrain, faunas, and floras, only a relatively few herpetological specimens were collected and these were deposited in the U.S. National Museum (Smithsonian Institution). Thus, it has remained for others to explore and report the rich herpetological faunas of this state. References to other important studies are cited in the first of this series (Tanner 1985 [1986]). One cannot traverse this area without becoming enamored with its rugged diversity and beauty. There are few areas where one can stand in a coniferous forest on the rim of a mighty canyon and observe an entirely different biome approximately a mile below, where wild figs and mangoes grow along a river, which is in turn surrounded by an invading thorn forest from the bench lands of Sinaloa (Fig. 1).

The climate in Chihuahua can be characterized by its cool to cold winters (November into March), dry to very dry springs (March through June), and moderately to heavily rainy summers (July into September), although the amounts will vary greatly from location to location and from year to year. The fall months (mid-September and October) are delightful, with warm days and cool nights. As indicated below, the climate and terrain combine to provide numerous habitats and a moderately rich amphibian fauna.

During the dry season (March through June) few amphibians are seen and those only along permanent streams and springs. Much of central Chihuahua is at an elevation between 5,000 and 6,000 feet; and, therefore, it is cool to cold until May with occasional frost during April. It is not until the summer rains come, usually from July to the first part of September, that an abundance of amphibians is seen. A trip from western Durango to Ciudad Chihuahua during a rainstorm corresponded with the emergence of large numbers of frogs and toads from areas that had

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Fig. 1. View from the west rim of the Barranca de Urique east of Cerocahui, Chihuahua, Mexico.

been very dry a few days before, but teemed with life soon after the heavy rain.

The following is from my field notes taken on 24 July 1958:

> Near El Salto, Durango, about 4:00 p.m. it began to rain. We decided to return to Chihuahua City and drove through the rain until 2:00 a.m. About 18.5 miles north of Durango City (and for the next 50 miles) we encountered large numbers of amphibians on the road, in the pools along the road and calling from the entire area, in concert, but with several distinct choruses. The following were collected: *Bufo d. insidior*, *Bufo cognatus*, *Hyla arenicolor*, and *Scaphiopus hammondi*. They were so numerous on the road that we could not drive without hearing a constant "pop" as their inflated bodies were crushed.

We outran that storm but were in it again at Ciudad Chihuahua on the afternoon of 28 July. The following is recorded in my field notes:

> Packed and left Chihuahua City about 4:00 p.m. in a light rain. The rain continued and intensified during our trip to Colonia Juárez. The amphibians were seen on the road for most of the trip. In some of the valleys between Sueco and Casas Grandes, we encountered large numbers of the same species seen in Durango.

The phenomenon of amphibian emergence after heavy late spring or summer storms occurs throughout many areas in North America. Inasmuch as I have seen the same phenomenon in Kansas (summer 1948), I would classify Chihuahua as a southern extension of the areas to the north and not an exception. A similar emergence occurred in the mountains at Chuhuichupa (3 July 1958) and was repeated again at Cerocahui (17 July 1958). In both cases *Bufo microscaphus* and *Hyla eximia wrightorum* were abundant.

Careful collecting was done around most habitats, such as small mountain streams, springs, seeps at the base of cliffs, and, in general, areas that serve as salamander habitats in southern Mexico. We found only one species of salamander, *Ambystoma rosaceum*, and concluded that the radiation of plethodontids had not extended north of Nayarit.

The discovery of *Pseudoeurycea belli* in eastern Sonora (Lowe et al. 1968), and more recently in adjoining west central Chihuahua, revives the belief that representatives of the Mexican plethodontids may indeed occur in select habitats along the western front of the Sierra Madre Occidental. The western mountains, which extend north from central Mexico, have served as dispersion pathways for representatives of major groups to reach north into Sonora and Chihuahua, as may be seen in such genera as *Eleutherodactylus* (*tarahumaraensis*), *Eumeces* (*brevirostris*), and *Thamnophis* (*melanogaster*), to mention only a few. Not only have these mountains provided a series of habitats conducive to dispersion, but they have also provided places of refuge from desiccation since the last pluvial period in an area now nearly surrounded by deserts.

We did not collect in all areas of southwestern Chihuahua. Those areas near the barrancas in western Chihuahua were not extensively worked. Thus, much must be done in these areas before we can present complete distributions of the species listed in this report.

Localities we visited are listed on the map published in the first report on the snake fauna. The map has been revised for reprinting in this report. It should be noted that most records are in areas outside of towns and cities. The map provides general locations and should aid in the identification of most localities cited in the text (Fig. 2).

Since our first trip into Chihuahua in the spring of 1956, considerable change has occurred in some of the waterways. This has undoubtedly affected habitat areas along streams in the central area. Dams have been built along some streams, particularly in the fertile valleys of central Chihuahua. This occurred basically in the valleys directly east of the higher mountains to the west and has essentially eliminated some of the streams that originally flowed north into the catch basins of northern Chihuahua. Such streams as the Santa Carmen, Santa María, and Río de Casas Grandes provide little, if any, streamflow north of such towns as Rancho Flores Magon, Galeana, and Colonia Dublan. The diversion of streamflow has also eliminated most of the wetlands that were once a part of the areas adjacent to the streams.

This situation was also referred to by Conant (1974 [1977]: 485–89). To compound the difficulties, bullfrogs (*Rana catesbeiana*) have been introduced in some of the areas, thus interjecting a serious predator to other amphibians that may have originally inhabited ponds and streams in these valleys. Man's agrarian activities in these valleys and others to the south may actually provide additional habitat in some areas to partially compensate for the diversions that their activities have wrought on the northern parts of these valleys.

It should be noted that precipitation occurs in Chihuahua primarily during July, August, and early September, during which time heavy rains may occur as thunderstorms rather than as general rains that cover all or the major part of the state. These thunderstorms present a hit-and-miss pattern. Thus, the rainy season presents a climate characteristic of steppe deserts. It is during this time that the amphibians are most active, not only breeding but also, during the evening hours, feeding in open areas not always associated directly with streams or ponds. As noted above, the dry season in the spring and early summer provides little opportunity for most anurans to be active. Also, the evening temperatures may fall sharply in September or early October, thus terminating the period of activity as well as the feeding season at approximately three months for most species. In the species accounts additional ecological information is presented.

Because of the varied geographical terrain of the area studied, the amphibian fauna of Chihuahua may be placed into three rather distinct biotic groups as follows:

1. *Central Chihuahua*. This area includes the valleys, low hills, and mountain ranges lying between Highway 45 (Ciudad Juárez to Parral) and west to the Sierra Madre. This central part of the state is divided into two major drainage systems. The uplift of the Sierra Del Nido and the accompanying lower ranges extending west from Del Nido to the vicinity of Cuauhtemoc and Ciudad Guerrero serve to divide the northern system (Río de Carmen, Río Santa María, and Río de Casas Grandes) from the more extensive Río Conchos to the south and east. Extending into this central area are lower desert valleys and ranges of eastern Chihuahua (Conant 1974 [1977]). It should be noted that the Río Papigochic (a tributary of the Río Yaqui) enters west central Chihuahua through a low area in the Sierra Madre and drains some of the high valleys. The area extending north from

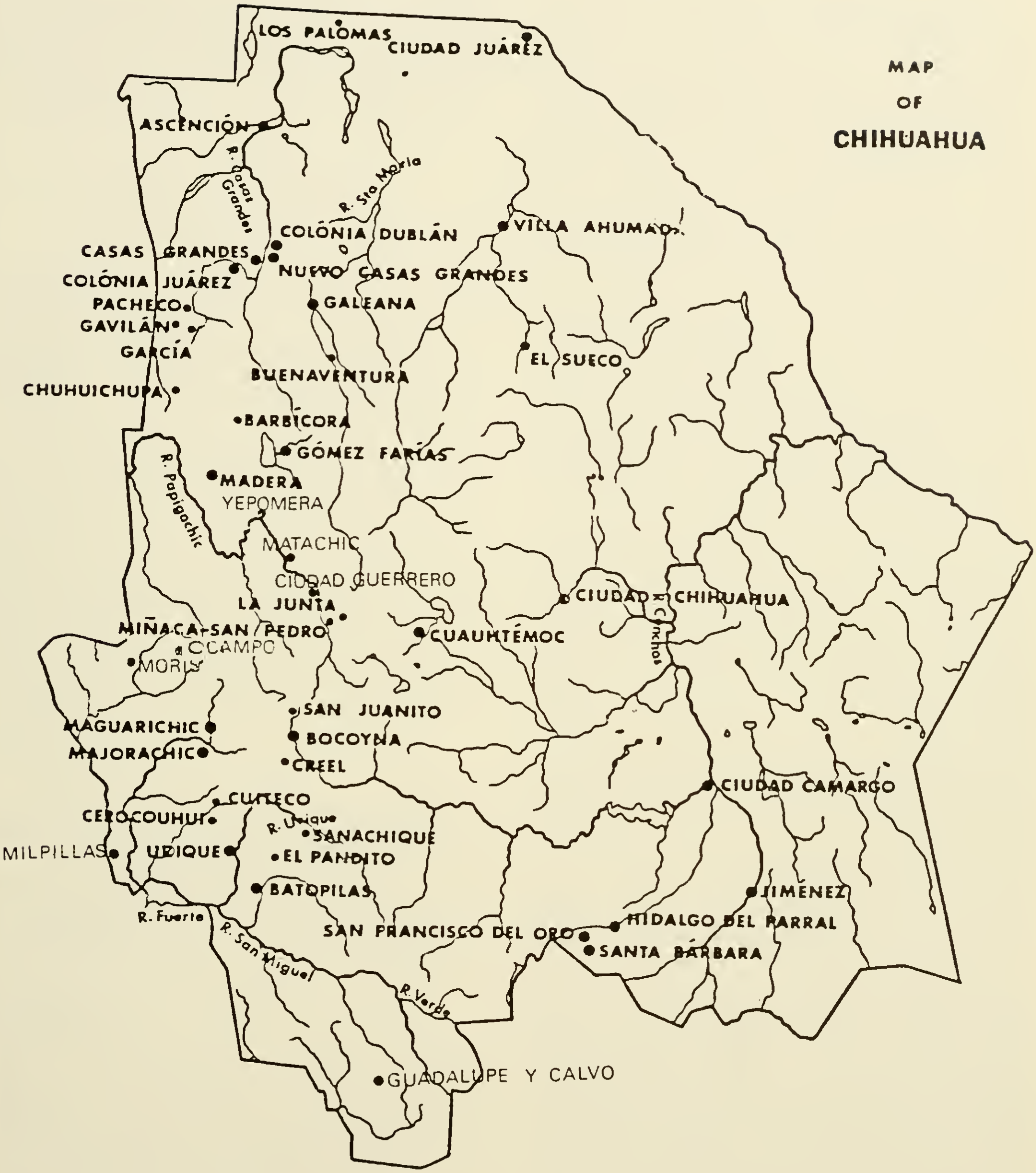
MAP
OF
CHIHUAHUA
LOS PALOMAS
CIUDAD JUÁREZ
ASCENCIÓN
R. Casas Grandes
R. Sta Maria
COLÓNIA DUBLÁN
VILLA AHUMADA
CASAS GRANDES
NUEVO CASAS GRANDES
COLÓNIA JUÁREZ
PACHECO
GALEANA
GAVILÁN
GARCÍA
EL SUECO
BUENAVENTURA
CHUHUICHUPA
BARBICORA
GÓMEZ FARÍAS
R. Papigochic
MADERA
YEPOMERA
MATACHIC
CIUDAD GUERRERO
LA JUNTA
CIUDAD CHIHUAHUA
R. Conchos
MIÑACA
SAN PEDRO
CUAUHTÉMOC
OCAMPO
MORIS
SAN JUANITO
MAGUARICHIC
BOCOYNA
MAJORACHIC
CREEL
CIUDAD CAMARGO
CUITECO
CEROCOUHUI
R. Urique
SANACHIQUE
MILPILLAS
URIQUE
EL PANDITO
BATOPILAS
JIMÉNEZ
R. Fuerte
HIDALGO DEL PARRAL
SAN FRANCISCO DEL ORO
R. San Miguel
SANTA BÁRBARA
R. Verde
GUADALUPE Y CALVO

Fig. 2. Revised map of Chihuahua.

Minaca to Yepomera and Madera is a part of the Río Papigochic drainage system.

Within this central area are found a series of species closely associated with the desert habitats to the north and east. The northern part of this area is basically a northwestern extension of the Chihuahuan Desert. It is our observation that the major populations of amphibians in this central area are found in the valleys, which are dry except during the rainy season but then, with the onset of heavy summer rains, literally erupt into breeding populations. This is in contrast to the few individuals seen along the small or intermittent streams during the dry season.

Those species most commonly seen in the central area are the following: *Scaphiopus couchi* Baird, *Bufo debilis insidior* Girard, and *Bufo woodhousei* Girard.

Some species have ranges that extend from the mountains into the lower river valleys and basins; *Spea hammondii* Baird, *Bufo punctatus* Baird & Girard, *Hyla arenicolor* Cope, and *Rana pipiens* Schreber are found, but our records indicate that they are less abundant in these lower valleys than are populations of these species in the higher valleys and western mountains. Records for *Rana pipiens* for 1931 are from Colonia Dublan (BYU 301 and 3657). We found them approximately 14 miles south of Casas Grandes. Bullfrogs were abundant at the river and springs near the old Rancho San Diego, downstream from Colonia Juárez. Apparently, *pipiens* had been greatly reduced or eliminated from most of the Río de Casas Grandes by bullfrogs and water diversion. This may be true for other species that were present in the recent past.

2. *Sierra Madre.* The second group, and perhaps the largest series, of species in Chihuahua occurs in the Sierra Madre. Mountain streams, meadows, and springs provide a variety of habitats that are less frequently found in the central areas of the state or are unavailable or unusable in the rapid streams of the deep barrancas to the west. The following are listed: *Ambystoma rosaceum* Taylor, *Spea hammondii* Cope, *Bufo woodhousei* Girard, *Bufo simus* Schmidt, *Bufo punctatus* Baird & Girard, *Eleuthrodactylus tarahumaraensis* Taylor, *Hyla arenicolor* Cope, *Rana pipiens* Schreber, and *Rana tarahumarae* Boulenger.

3. *Western barrancas.* In the western barrancas, particularly at Urique, two species, *Bufo marinus* and *Bufo mazatlanensis*, were abundant in the streets of the town and along the river in the evenings (14 July 1958). Other species occurring in northern Sinaloa and southern Sonora may enter the mouth of the barrancas in extreme southwestern Chihuahua. We collected one specimen of *Bufo punctatus* at Urique and a small series at Cerocahui and Cuitaco, an indication that this species has also entered the lower basins of the Río Oteros. A single representative of *Pachymedusa dacnicolor* Cope was examined by Peter Warren on 4 January 1980, approximately 5 km south of the junction of the Río Chico and Río Yaqui. This is about 50 km by air northeast of Ciudad Obregón, Sonora. Its presence in the Río Yaqui suggests its presence in western Chihuahua. From the few records available it is obvious that the areas along the state borders between Sonora, Sinaloa, and Chihuahua are not well known. Thus, the distributions of many amphibian and reptile species are not as yet defined.

SPECIES ACCOUNTS

Family Ambystomatidae

Genus *Ambystoma* Tschudi

Ambystoma rosaceum Taylor

Ambystoma rosaceum Taylor, 1941, Copeia 1941: 143–144, Figs. 1A, 1B. Type locality: Majorachic, Chihuahua, Mexico; Anderson 1978: 206.1-.2.

In small side streams of Río Bavispe, below Tres Ríos near Chihuahua-Sonora border, 4 larvae (BYU 13727–30).

Approximately 15 mi W Pacheco (Río Gavilan), 1 (BYU 16877 small adult S-V 50.8 mm).

18–20 mi from Colonia Juárez up Tinaja Canyon, 14 (BYU 14417–30, larvae).

Nortena, 5 mi NW Chuhuichupa, 35 (BYU 14432–66, larvae with one transforming–14442).

1 mi S Chuhuichupa, 8 (BYU 13942–44, 14414, 4 recently transformed adults ranging from 44.0 to 69.5 mm in S-V length; 14488–91, larvae, 30.0–42.5 in S-V length).

Black Canyon approx 8 mi W Chuhuichupa, 3 (BYU 14256–58, larvae).

10 mi NW San Juanito, 2 (BYU 14483, 15684, larvae).

8 mi SW Maguarichic, 11 (BYU 16879–89, larvae).

25 mi SE Creel, 34 (BYU 17110–28, 22771–22794, all larvae, 32.0–42 mm S-V length).

8 mi N Basihuari, 12 (BYU 22646–57, 1 adult 51.0 mm S-V and larvae 34–47 mm S-V length).

15.5 mi N Basiberachic, 11 (BYU 22747–57, larvae).

9 mi SE Colonia García, 1 (MVZ 20681, adult).

Del Nido, Arroyo Mesteno, 19 (MVZ 70554–59, adults; 68714–20, 65939–41, 70547, 70552 larvae).

Río Milpillas, 1/2 mi S Milpillas, 1 (UAZ 45882, small adult, S-V 57 mm).

Arroyo la Cienega Prieta, approx 1.5 mi N Las Chinacas (N of Milpillas), 1 (UAZ 46562, larvae S-V 55 mm).

14 mi SE Madera (Hwy 16), 1 (UAZ 34641, adult male).

4.6 mi SE Madera (Hwy 16), 1 (UAZ 34642, adult male).

Yepomera, 2 (UAZ 34777–8, adults).

2 mi S Yepomera, 1 (UAZ 34779, adult).

6.8 mi NW Yepomera, 1 (UAZ 34780, adult).

Mpio, Guadalupe y Calno, E side of Cerro Mohinora, 3,750 ft, (UTEP 9307, 1 adult, 73.5 mm S-V, and one lot of 20 larvae).

8 mi E Guadalupe de Los Reyes (29.1 mi E Cosala, Sinaloa), 1 (UAZ 46090, this locality is approx 75 mi NW of El Salto, Durango, larva-S-V 65.2 mm).

Neviera, 4 mi W La Ciudad, Durango (MVZ 47288–9, 57274, 57276–57291, 58648–63, 65890, 22 adults and 14 larvae).

Río Hondo near Los Adjuntas, Durango, 1 (MVZ 57305, larvae).

11 mi W El Salto, Durango, 1 (USNM 154571, adult).

El Salto, Durango, 1 (USNM 123581, larva—type of *Ambystoma rosaceum nigrum* Shannon).

SW of Ciudad Durango, 1 (CAS 87350, larva).

Specimens collected in Durango are indicated; all other collection citations are from the state of Chihuahua. This salamander is present in nearly all small streams, springs, and ponds throughout the mountains of western Chihuahua. We did not find it in the larger streams and rivers where fish occurred. They are more commonly observed in habitats 6,000–8,000 feet in elevation, although some descend into the canyons and high valleys such as the Tinaja and Yepomera, to at least 6,000 feet. We observed the life history from eggs to transforming larvae and two breeding adults. Although some aspects are not yet clearly understood, the life history data available from our studies are reported in the following sections.

Eggs and Larvae.—Eggs were first observed on 2 April 1963 in large potholes in Tinaja Canyon approximately 18 miles northwest of Colonia Juárez. The potholes were fed by seeps along the floor of the canyon and were filled with large, embedded boulders. Eggs were found in two clear ponds, both 2–3 feet deep. In my field notes, the following is recorded:

> In two potholes there were eggs, in one they were attached between two large rocks (boulders), some were hatching, some out, others not. There were 20–25 eggs and larvae. In the second pool, eggs were laid on tree roots that were extending out and down into the pool. The eggs were attached in clusters of 2–7. On the opposite side of this pool, on the lower edge of a large boulder, 30 eggs were securely attached to the surface of the rock. None of these were hatching. In this pool, a large cluster of frog eggs (*Rana*?) was found.

Because the boulders were large and embedded, we could not investigate for additional eggs or adults that may have been beneath (Fig. 3).

On 3 April 1963, at a small spring, we found eggs and two adults. This spring and small stream is called the Turkey Tank and is a small tributary of the Río Juárez. The locale is about 15 miles southwest of Colonia Juárez and a short distance off the road to Pacheco. Only potholes were filled with water, with the small stream filtering through sand and gravel leaving little exposed water. Here, as at Tinaja, only potholes provided one to two feet of clear water, and in two of these, eggs were attached to rocks, pine needles, and other debris. Here also the eggs were in clusters of 3–4 to as many as 10–12. Some were also in strings of 3–6 eggs. Eggs were scattered over the rocks in an irregular pattern but with each cluster securely attached.

Eggs and/or large adults were not found during our field studies from mid-May to late July and August. During this time only larvae and small transforming adults were seen. Anderson (1961) states that "mating probably occurs soon after the onset of the summer rainy season, which would be any time from mid-June to mid-July in Durango and Chihuahua." I have no data for Durango, but in Chihuahua most eggs are laid during April or perhaps during early May in the higher elevations (Webb and Baker 1984). This is not to say that some eggs may not be laid during the first heavy rains of July. In our study of *Ambystoma tigrinum nebulosum* in Utah (Tanner et al. 1971) the breeding season occurred in May as soon as the melting snow filled the ponds. However, after a heavy July rain a few adults were seen in the lake, and by August we noted that there were large and small larvae. We suspect that this may occur in *rosaceum*; however, the observations of Anderson (1961) at Yaguirachic and those we have made only indicate the possibility of such an occurrence.

In Chihuahua, March through June is the dry season. During this period large larvae would have difficulty securing food in the limited aquatic habitats, but small larvae are able to establish themselves so that by the onset of the rainy season they are greatly benefited by the increased feeding areas provided by the rains. Unfortunately, I do not have precise data on the rate of growth by larvae. What is known is that eggs are laid much earlier than July and that small larvae 20–30 mm snout-to-vent length are found in May (Tinaja and below Tres Ríos). By mid-July and into August, some larvae are 45–55 mm and some are transforming into small adults with a snout-to-vent length ranging from 44 to 54 mm

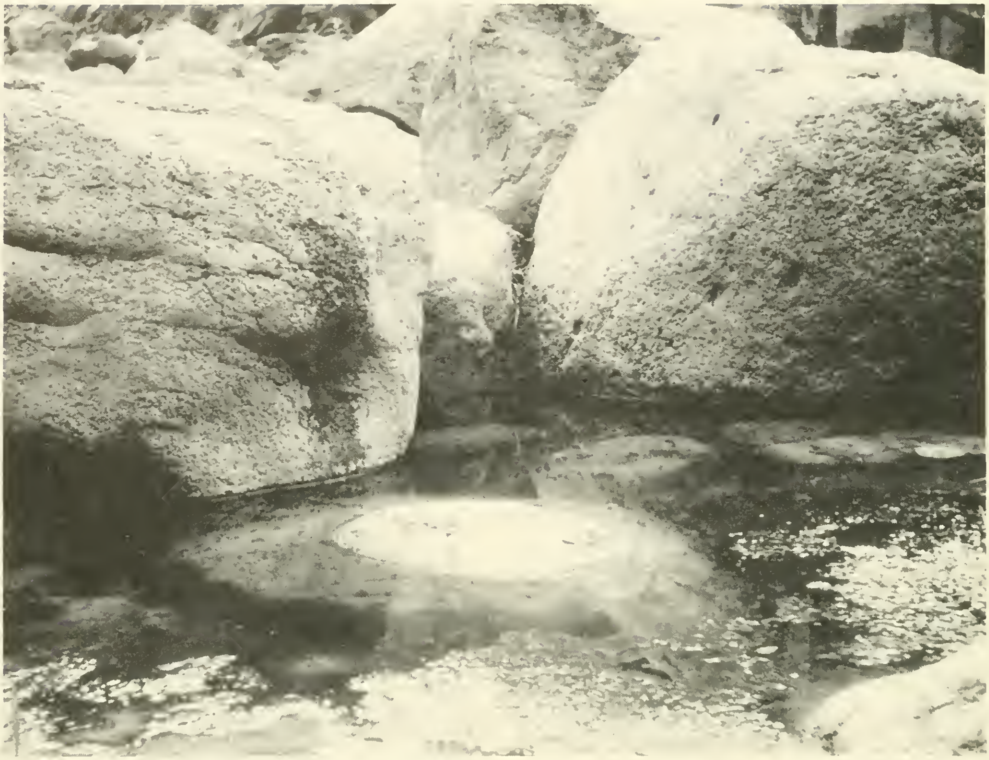

Fig. 3. An example of potholes along the streambed in upper Tinaja Canyon. This photo was taken 28 May 1956.

(Fig. 4). Our data do not indicate that larvae winter over to the next July as was suggested by Anderson (1961) and Anderson and Webb (1978). All data available to us strongly indicate that the majority of populations of *rosaceum* in Chihuahua grow from larvae spawned in April and transform into small adults before the onset of winter. Our observations of populations in the higher habitats suggest that the observations at Yaguirachic by Anderson were not at variance with ours at Chuhuichupa and that the larger larvae were probably spawned in April or early May. We did not find large larvae in any habitats (Tinaja or Tres Ríos) during April or May. I believe that *rosaceum* has adapted to an early breeding season even though the aquatic habitat in most areas consists of seeps and small streams and is thus limited in space until the rains arrive. Furthermore, small larvae would be at a great disadvantage during the rainy season when the heavy runoff usually occurs. Therefore, an early breeding season provides limited but adequate water in the habitat for small larvae. By July larger larvae can cope with the increase of streamflow and, as noted above, a greater feeding area and perhaps a greater abundance of food. July appears to be a period of rapid growth, resulting in larvae that reach their full growth and transform

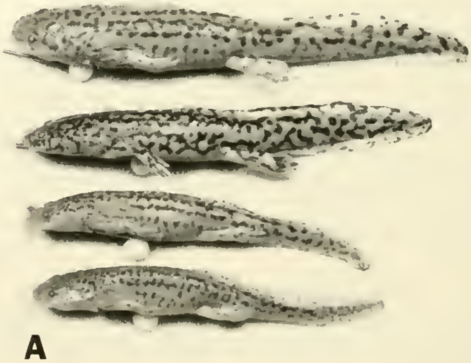

Fig. 4. Selected *Ambystoma r. rosaceum* larvae from the mountains of western Chihuahua, eastern Sonora, and Sinaloa: A, Chuhuichupa, July 1958, S-V 30–40 mm. (Figs. 4B through 4D continued on facing page.)

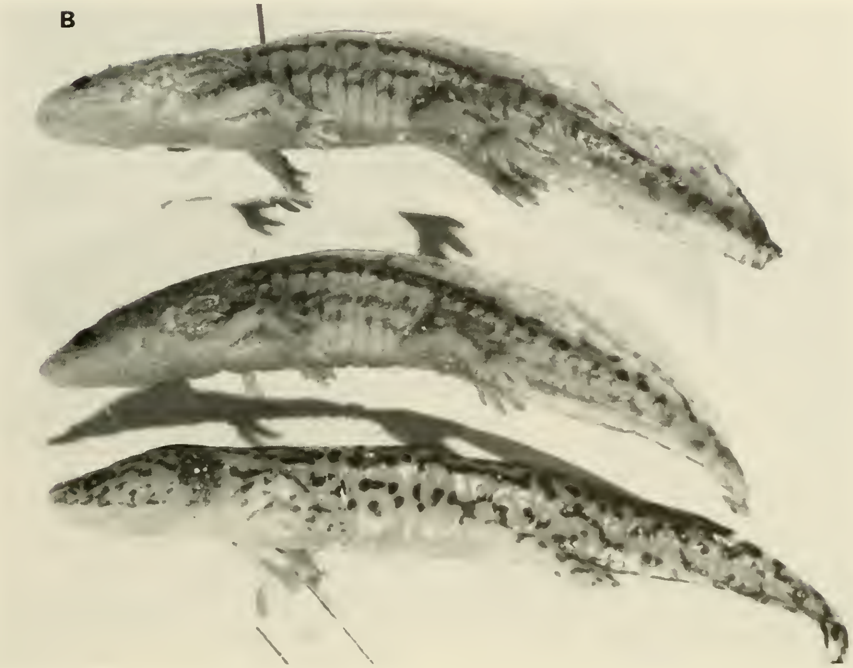

Fig. 4B continued. Chuhuichupa, 25 August 1957, S-V 45–50 mm (dorsal fin and gills reduced).

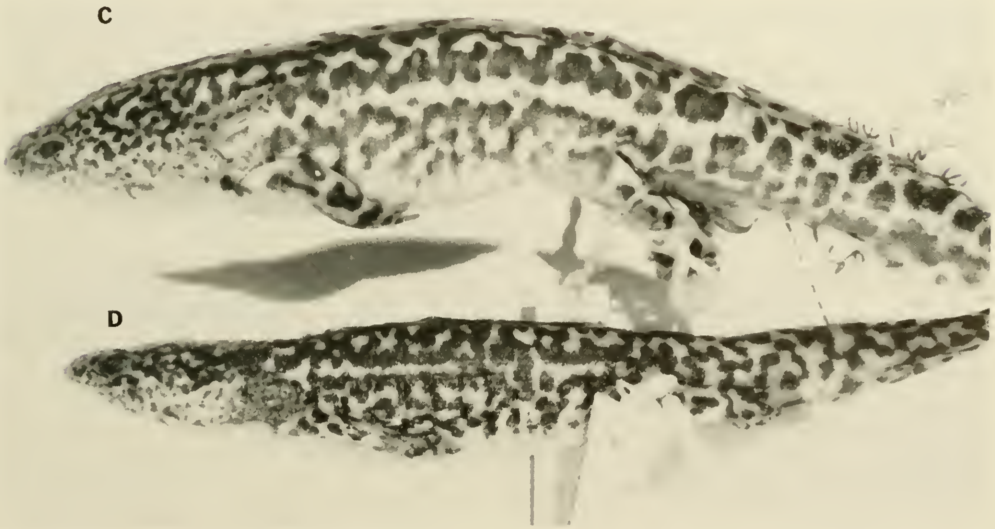

Fig. 4C, D continued. C, 25.15 mi (by road) N Yecora, Sonora, UAZ 45879, S-V 58.2 mm; D, 48.2 mi NE Mocorito along road to Surutato, Sinaloa, UAZ 46091, S-V 54.8.

during August or at the close of the rainy season in September or October (Fig. 4).

Webb and Baker (1984) found eggs and small larvae in late May. These were in permanent streams and consisted of small and large larvae (at an elevation above 10,000 ft, locality 3, northeast side of Cerro Mohinora, ca 3,750 m). As noted above, elevation may delay egg laying until May and also increase the time needed for larvae to transform.

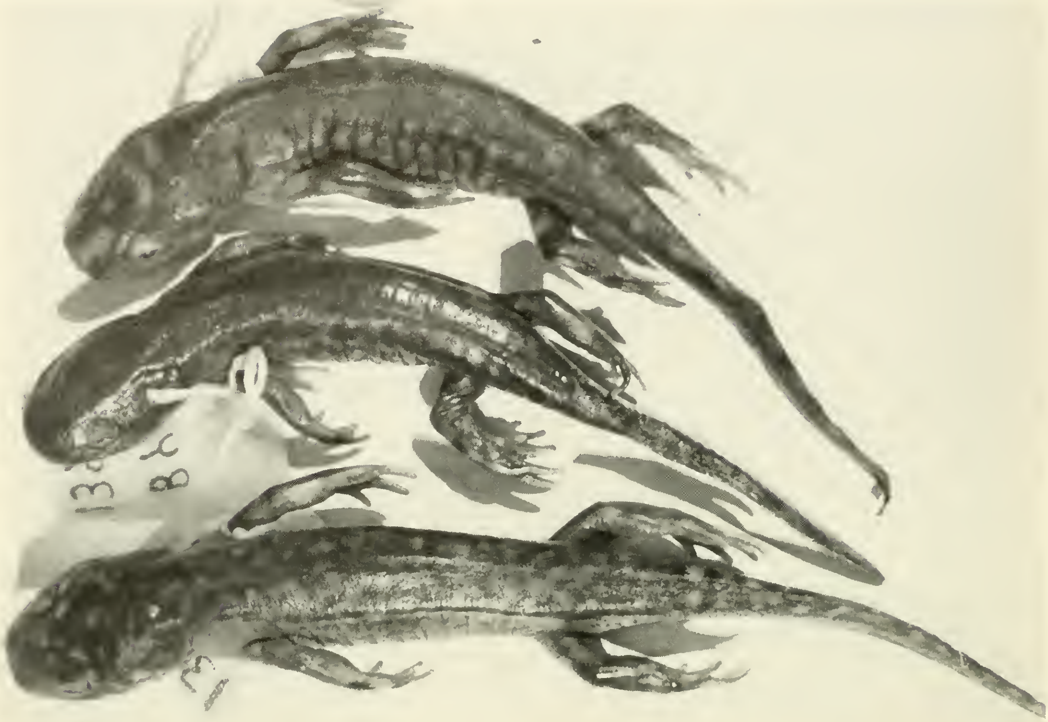

Fig. 5. Recently metamorphosed adults of *Ambystoma r. rosaceum* collected 1 mi S of Chuhuichupa, Chihuahua, 25 August 1957. BYU 13943, 13944, and 13942; S-V 45.2, 44.7, and 51.8, right to left.

NEOTENY.—We observed no neoteny in the *rosaceum* of Chihuahua between 1956 and 1972. We saw no large larvae during April (1963 and 1985) and May (1956) in habitats where we found large numbers of them in July and August. There were perhaps two basic reasons for this: It is (1) too dry to provide a habitat that would permit survival or (2) too cold to allow wintering over. Under these conditions, adults survive by burrowing, whereas neotenes cannot. Our data strongly suggest a life cycle of early egg laying (April and perhaps May) with little breeding at later dates (July), a rapid growth of larvae, particularly after the onset of summer rains, and a period of metamorphosis from mid-July into October with little or no carryover of larvae in most, if not all, habitats even in the higher mountains of western Chihuahua. That breeding larvae occur in Durango and Sinaloa is not questioned, but we did not find them in western Chihuahua and can find no data in the reports of Anderson (1961) or Anderson and Webb (1978) to support their occurrence. Webb and Baker (1984) report large larvae in late May. This indicates a wintering over of larvae but does not confirm larval reproduction since adults were also present.

ADULTS.—Two mature adults and 10 transforming or recently transformed adults were collected (Fig. 5). The latter ranged in size from 44 to 53 mm S-V, one adult 69.5 mm (Fig. 8). During late July and August numerous larvae were observed with reduced gills and the dorsal fin greatly reduced or absent from most of the body. Time limits precluded our gathering data on the length of time involved in the process of metamorphosis. Individuals with only stumps of gills were seen along the edge of the water or out on the bank.

Apparently, *rosaceum* has adapted to take advantage of the rainy season. The larvae, having reached the size and age for metamorphosis, are ready to leave the aquatic habitat while the terrain is moist. Thus, the new terrestrial habitat is less stressful, having a moist ground litter and softer soil for burrowing.

Two breeding adults were collected at the Turkey Tanks (3 April 1963). In our attempt to return them alive they died and spoiled while

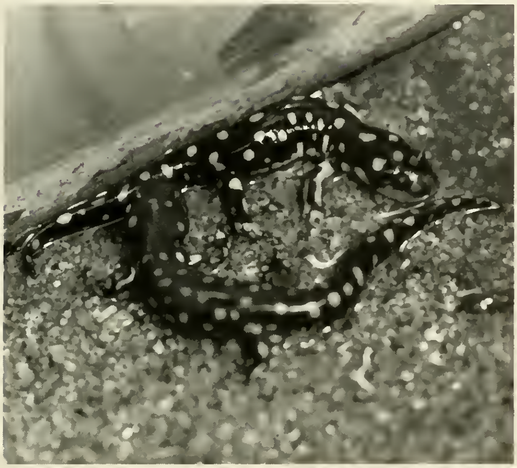

Fig. 6. Adult *Ambystoma r. rosaceum* taken at the Turkey Tanks SW Colonia Juárez, 3 April 1963.

in transit. The pair was marked with yellowish cream spots and blotches on a dark greenish ground color. Their general appearance was reminiscent of *Ambystoma tigrinum tigrinum* except that the spots were more uniformly round and small (Fig. 6). The smaller and perhaps younger adults still retained some features of the larval pattern (Fig. 5). One transforming specimen was returned alive to the laboratory where it slowly developed the yellowish spots similar to the breeding adults from the Turkey Tanks (Fig. 7). The laboratory specimens readily accepted earthworms.

The series of specimens from Guadalupe y Calvo (adult, UTEP 9307 and lot 9308, 20 specimens) is important in that all specimens are from an area in southern Chihuahua and near Durango. Furthermore, the series consists of individuals ranging in size from small larvae, less than 20 mm in total length, to a mature larva, 51.3 mm S-V with gills and dorsal fin reduced. There is also a recently metamorphosed adult 53.0 mm S-V.

The series (collected 23 May 1982) is remarkable in that it contains all stages in the life cycle. Collections made in northern Chihuahua (25–31 May 1956) at Río Bavispe and seen in Tinaja Canyon were of a nearly uniform size (30–40 mm). I have observed little variation in the color pattern of the adults and larvae from Chihuahua. The degree of pigmentation may vary, some darker than others, but the pattern is essentially the same in all. However, in widely separated populations there may be some variation in the life cycles.

SYSTEMATICS.—Dunn (1940) included six adults and four larvae from Chihuahua (no localities or collections are listed) under the subspecies *Ambystoma tigrinum velasci*

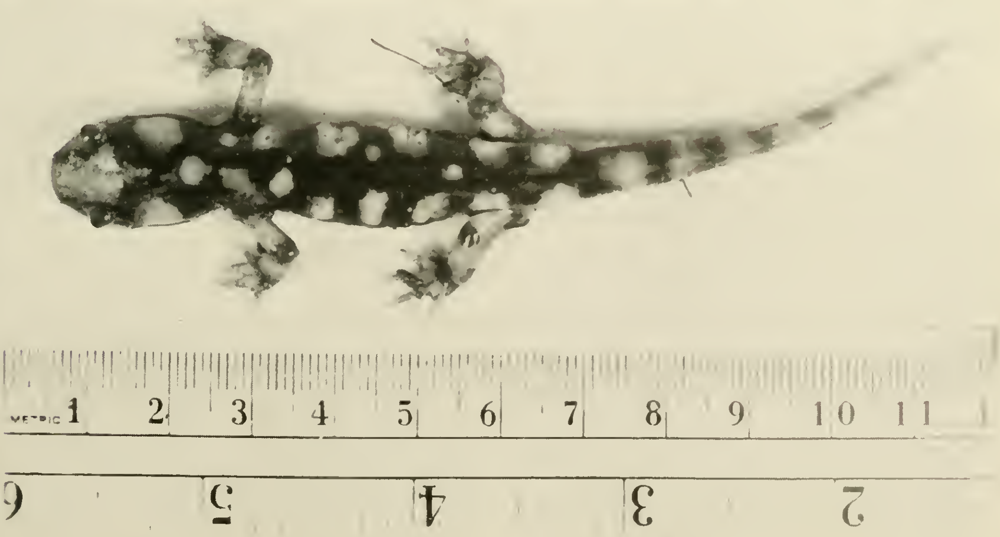

Fig. 7. Small adult collected (19 July, 25 mi S Creel) while still with gill buds and larvae color pattern. Returned to the laboratory where it developed the adult color pattern. Photo taken mid-September 1960.

Dugès. He described them as being "marked with round yellow spots and a high gill raker count" (9–15 gill rakers on the anterior face of the third arch).

In his closing remarks Dunn (1940) states, "Some specimens from Arizona and New Mexico with circular yellow spots cannot be assigned." He further states that "this form has rather large larvae with 19–20 gill rakers on the anterior face of the third arch, thus differing from *A. t. velasci.*" The specimens in question were from Prescott, Arizona (2); Río Mimbres near Deming (1), Ft. Wingate (9), Pescao (3), and Nutria (2), all from New Mexico. The location of these specimens was not indicated. It is obvious that he examined more material from Chihuahua and areas immediately to the north than had been done in previous studies.

Taylor (1941) described *A. rosaceum* (based on larval characters) and made no reference to the study by Dunn (1940). Shannon (1951) described the subspecies of *rosaceum*, *r. nigrum* from Salto, Durango, and *r. sonoraensis* from 32 miles south of the Arizona border, Sonora. Both Shannon subspecies were based on larval specimens.

Anderson (1961) reviewed the life history and systematics of *A. rosaceum*, concluding that the two Shannon subspecies were not valid. His reasoning was an extension of Dunn's (1940) concern that larval characters were not reliable in a final determination of *Ambystoma* taxa. Apparently, Anderson and Webb (1978) were still of the same opinion.

I agree with the conclusion reached by Anderson (1961) that *Ambystoma fluvinatum* Taylor is a color phase of *rosaceum*. The type of *fluvinatum* as figured by Taylor appears to be an individual in an early state of metamorphosis, with the dorsal fin greatly reduced. I have seen one of the larvae in the type series of *A. r. sonoraensis* Shannon (USNM 17255) and have compared it to specimens from the Río Bavispe drainage. In most characters there are only slight variations. However, the color pattern is of a more diffuse lateral pattern and there are fewer gill rakers (20) than in the Bavispe series (22–26).

Shannon (1951) described the color pattern as a "dark brown, ground color extends to edge of, but not or barely onto venter—otherwise pattern similar to that of *A. r. nigrum.*" We have noted significant differences in color patterns between the above description and specimens collected during our field trips into the Río Bavispe drainage system (below Tres Ríos, Chuhuichupa, and Black Canyon). We, therefore, assumed that *Ambystoma rosaceum* had developed a series of subspecies because of isolation in the major river systems. It is reasonable to suggest that the Río Bavispe, a tributary of the Río Yaqui, may contain populations as distinct as those in northern Sonora (*sonoraensis*), the Río El Fuerte (*rosaceum*), or the Durango subspecies (*nigrum*). We did describe and differentiate the larvae of the Bavispe area but hesitated to complete the report until a series of adults from the river systems are available. The teeth of six larvae were examined. The larval specimen (BYU 13727, S-V 44.7) is representative of the series and has the following: pterygoid 11, vomerine 20, premaxillary 13–14, maxillary 12–13, dentary 28, splenial 35, max-premax 35–27, dent-splenial 62.

Van Devender (1973) and Van Devender and Lowe (1977) reported the occurrence of *Ambystoma tigrinum* and *Ambystoma rosaceum* in the environs of Yepomera, Chihuahua. The adults were identified as *tigrinum* and the series of larvae taken from the streams and springs as *rosaceum*. This cells into question the presence of two ambystomid species (larvae of one and adults of the other) in the same habitat.

During a recent meeting with Dr. Charles Lowe, we examined the series of adults from the area in and near Madera and Yepomera, Chihuahua, which were reported by Van Devender (1973) and Van Devender and Lowe (1977) as *Ambystoma tigrinum*. We concluded that this series represented only adults of *Ambystoma rosaceum*. There is reason to believe that the occurrence of adults with bright yellowish spots did not correspond to the description of *A. rosaceum* as described by Anderson (1961). Furthermore, Dunn (1940) had referred spotted specimens from Chihuahua as representatives of *A. tigrinum*. Most, if not all, of the mature adults seen by Anderson (1961) were the dark subspecies from Durango, with most of his Chihuahua specimens being larval or small, recently metamorphosed adults. Thus, the finding of large greenish adults with bright, round, yellow spots was not expected to be *Ambystoma rosaceum*. Futhermore, Lowe (1964) and

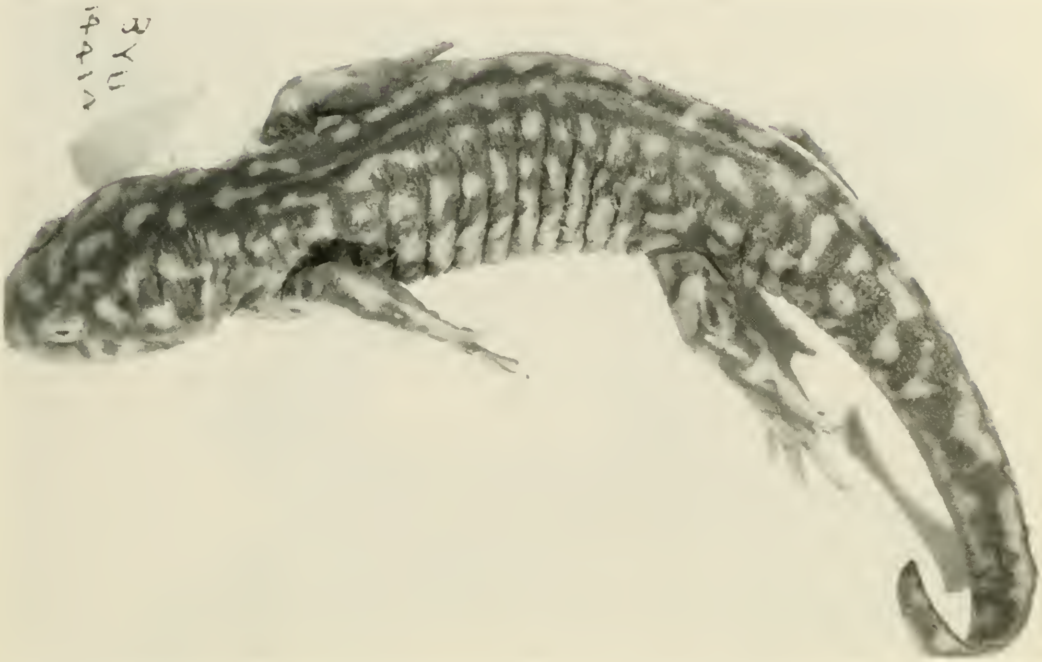

Fig. 8. *Ambystoma r. rosaceum* collected 1 mi N Chuhuichupa, Chihuahua, 2 July 1958. This was the largest recently transformed specimen collected, S-V 69.5, BYU 14414.

Webb and Roveche 1971 listed only *Ambystoma tigrinum* for Arizona and New Mexico.

The biology of *Ambystoma rosaceum* as stated above has a direct relationship to its systematics. It appears that eggs are laid in April and/or May. Larvae grow rapidly, with some reaching 45–55 mm in S-V length by late July and others by the end of the rainy season in September. Larvae begin to transform in July, retaining for a time the larval color pattern, and slowly develop a uniform darker color before the yellow spots appear that are characteristic of mature adults (see Figs. 5, 7). These data are for Chihuahua populations taken from areas west of Colonia Juárez and south to Maguarichic and areas near and southeast of Creel. Throughout this mountainous area, little variation occurred between the larval populations. Transforming specimens from Chuhuichupa and south of Creel developed similarly from mature larvae to young adults, with the mature color pattern of yellow spots appearing at 55–60 mm in S-V length.

Specimens collected at Chuhuichupa on 25 and 26 August 1957 included four recently transformed adults, 44–53 mm S-V. On 2 July 1958 we collected one specimen, 69.5 mm S-V, that still had three gill buds on each side; it was the largest one we collected or saw that had larval characters (BYU 14414, Fig. 8). These specimens were taken from and around the large springs south of town. All other larvae or transforming adults collected or seen were smaller (45–55 mm in S-V length).

A collection from 8 miles north of Basihuari (southeast of Carmen Bridge in Río Urique drainage) consisted of 12 specimens collected 4 October 1964 and included one small adult (51.0 mm S-V), one with reduced gills and dorsal fin greatly reduced (47 mm S-V), and a series of 10 larvae ranging in size from 34 to 45 mm. All were spotted and with a yellowish ground color. One can only speculate as to the age of these larvae. Other data suggest that eggs for these were laid in May. However, it is obvious that the larger individuals were transforming and that this would continue until the aquatic habitat was reduced or disappeared after the rains stopped and the soils dried.

A small adult from 1/2 mile south of Milpillas (UAZ 45882) in west central Chihuahua near the Sonora border and from the Río

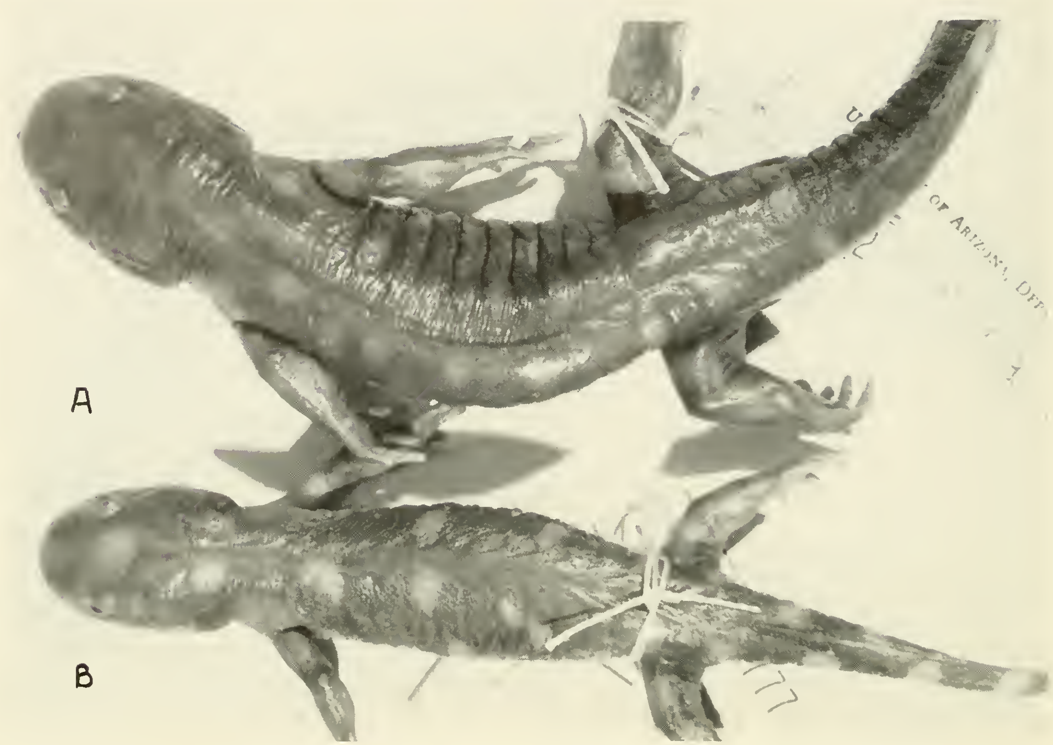

Fig. 9. Adults of *Ambystoma r. rosaceum* Taylor: A, male, UAZ 34642, collected 1 July 1971, 4.6 mi SE Madera on Hwy 16, Chihuahua, S-V length 89.0 mm; B, female, UAS 3477, collected at Yepomera, Chihuahua, 12 June 1972, S-V 75.5 mm.

Milpillas drainage has the round, light spots but with a dark ground color. It is possible that adults from Sonora may be spotted, but with a melanistic ground color, in contrast to the Chihuahua populations and the nearly spotless populations in Durango.

Although additional data from larger series of adults would be helpful, there are at present adequate materials available, both larvae and adults, from Chihuahua and Durango to recognize the following subspecies:

Ambystoma rosaceum rosaceum Taylor
Tarahumara Salamander

Ambystoma rosaceum Taylor, 1939 (1938). Univ. Kansas Sci. Bull. 25: 385–405.

This subspecies is distinguished by bright yellowish spots on an olive green ground color in adults (Figs. 6, 9). Larvae have dark spots and reticulations on a yellowish ground color that may be tinged with a pinkish color and with a lateral, irregular, yellowish stripe in the lateral line area.

It is presently known from the high valleys and mountains of western Chihuahua, mountains of eastern Sonora, and the drainage of the Río Sinaloa in northeastern Sinaloa and southern Chihuahua. The type locality is Mojarachic, Chihuahua. This distribution does not include northern Sonora north and west of the Río Yaqui drainage.

Ambystoma rosaceum nigrum Shannon
Durango Salamander

Ambystoma rosaceum nigrum Shannon, 1951. Proc. U.S. Nat. Mus. 101(3284): 465–484.

This subspecies is distinguished by a dark ground color without the bright yellow spots. Any spots are faint and in most individuals are indistinguishable in adults. Larvae have small, irregular, light spots and reticulations on a dark ground color; the central lateral light stripe may or may not be present (Fig. 10).

It is presently known from the mountains of west central Durango and east central Sinaloa. The type locality is El Salto, Durango.

REMARKS.—At present we do not have all the data that would detail the complete life

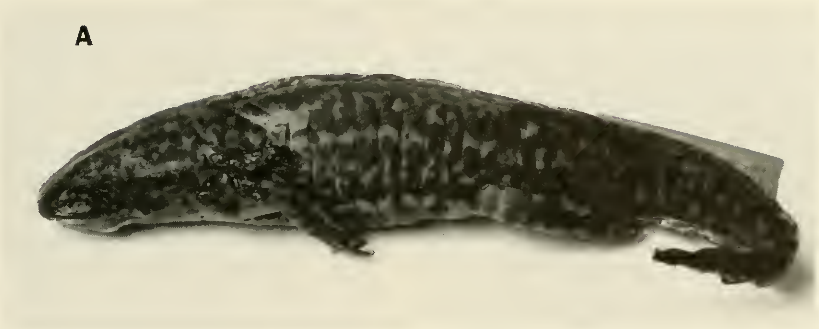

Fig. 10. *Ambystoma r. nigrum* Shannon: A, holotype (larva), USNM 123581, El Salto, Durango, S-V 59.0 mm.

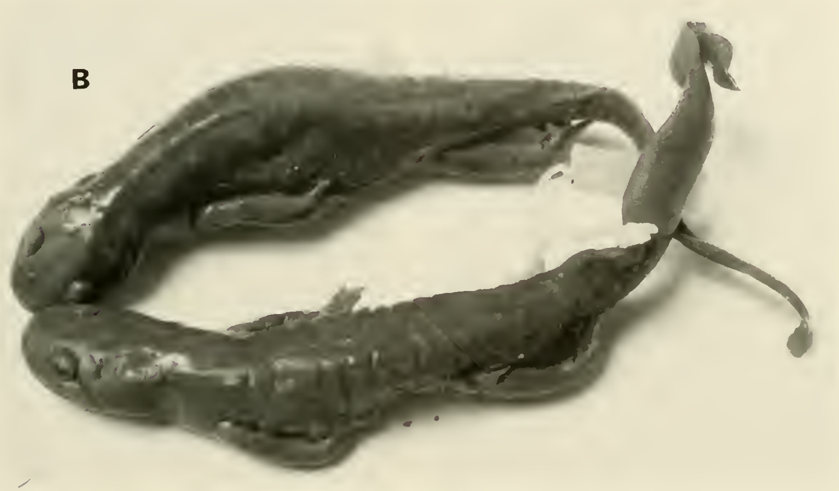

Fig. 10. *Ambystoma r. nigrum* Shannon: B, adults MVZ 57285, S-V 78.0, and 57279, S-V 72.8 collected at Neviero, 4 mi W La Ciudad, Durango.

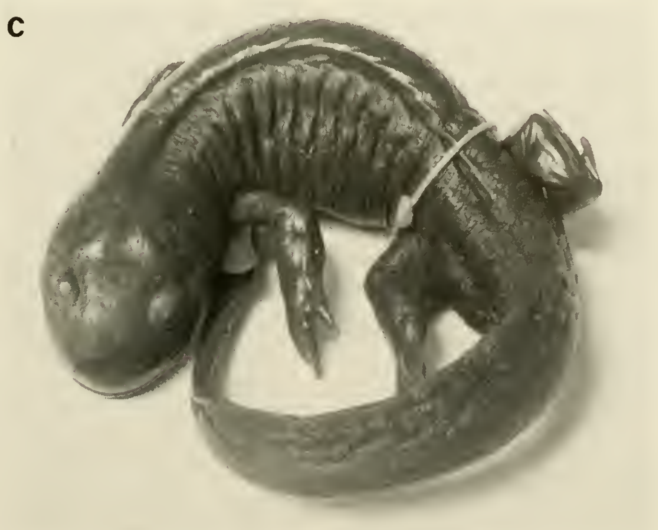

Fig. 10. *Ambystoma r. nigrum* Shannon: C, adult USNM 154571, collected 11 mi W El Salto, Durango.

history of *rosaceum* from egg to mature adult. Such a study presumably would provide details of the size of larvae from hatchling to one transforming, rate of larval growth, age and size of larvae at metamorphosis, and size of breeding adults in the subspecies. Only parts of this sequence are now fully understood. In spite of life history gaps that must yet be filled, data now available do provide a more complete understanding than has been available.

It is obvious that elevation plays an important role in determining the time of egg laying. In Sinaloa (Sierra Surutatas, 48 airline km northeast of Guamuchil, about 3,500 ft) Anderson and Webb (1978) report that eggs were laid in February. We found eggs in Chihuahua in April at about 6,000 ft; Webb and Baker (1984) found them in May on the northeast side of Cerro Mohinora at about 10,000 ft.

Whether eggs are laid in late June or July at the onset of summer rains as suggested by Anderson (1961) has not as yet been observed in Chihuahua populations. Our data suggest that this does not often occur for the following reasons: (a) competition with the larger larvae and life in the increased streamflow, at times in flooding channels, would make survival difficult in many habitats; (b) egg laying that late in the year may not provide enough time for growth and metamorphosis before the water in most habitats is reduced or disappears soon after the close of the rainy season. However, as noted above, other ambystomatid species are known to be stimulated to reproduce late in the season after heavy summer storms, and, though this has as yet not been observed in the *rosaceum* of Chihuahua, it may occur.

The suggestion of Dunn (1940) and Anderson (1961) that larval characteristics are too variable to be useful in systematics may have merit. However, I find that the larvae of *Ambystoma rosaceum* do have a very distinctive color pattern. Both Taylor (1941) and Shannon (1951) used larval characters in establishing and differentiating taxa. Variability should not be a justifiable criterion for eliminating the usefulness of characters that may appear in the sequence of a species' life history.

The external anatomy of *Ambystoma rosaceum* as it appears in the text was prepared before studies dealing with electrophoretic data were reviewed. It is of interest to note that both studies (Shaffer 1983 and Jones *et al.* 1988) arrive at essentially the same conclusions, namely that *rosaceum* is a species distinct from *tigrinum*. Shaffer also concluded that *rosaceum* is a polytypic species with *A. r. rosaceum* in the north (Chihuahua) and *A. r. nigrum* in the south (Durango).

Family Plethodontidae

Genus *Pseudoeurycea* Taylor

Pseudoeurycea belli sierraoccidentalis
Lowe, Jones, & Wright
Pine-Oak Plethodon

Pseudoeurycea belli sierraoccidentalis Lowe, Jones, & Wright, 1968, Contributions in Science, Los Angeles County Museum 140: 1–11. Type locality 21 km WSW Yecora, Sonora.

6 km WNW Ocampo (on road to baseball field El Aguila) (Lowe, Van Devender, and Holm, in press).

Four adults were observed on 24 June 1987 by field parties on a trip organized by Paul S. Martin of the University of Arizona. The specimens were emerging from holes in rotted tree roots in the bank of a road cut. Above the road cut is a pine-oak woodland with volcanic boulders and deep leaf litter. The elevation is approximately 1,830 m.

Pseudoeurycea b. sierraoccidentalis is a black salamander with dark red spots on its upper surfaces. Ground color above is a uniform black throughout with little variation between the dorsal and ventral areas. The number of spots for three of the Ocampo animals was 0, 11, and 13, based on field notes and color slides; field photo specimen vouchers are UAZ 47824–25 PSV. The samples include the first spotless individual for the species.

The area of Ocampo, Chihuahua, and the type locality southwest of Yecora, Sonora, are in the headwaters of the Río Mayo. These uplands range above 6,000 ft and are near, if not a part of, the divide between the Río Mayo and Río Yaqui drainage systems. Furthermore, the drainage basins to the east (ca 50 km) include the headwaters of streams flowing north into the Río Yaqui or south into the Río Fuerte (Oteros). This suggests a much larger distribution than is now known for both eastern Sonora and west central Chihuahua.

The type locality and habitat of the type series is in an east-west oriented canyon (barranca) with the upper end extending into an area in or near Chihuahua (Lowe et al. 1968). Thus, the western slopes of the mountains extending from about 5,000 feet in Sonora to at least 6,000–7,000 ft in west central Chihuahua are apparently the present habitat.

Family Pelobatidae

Within this family are genera from a wide distribution that includes representatives from Europe to the South Pacific. In North America only the genus *Scaphiopus* is presently recognized by most authors (Tanner 1939, Zwiefel 1956, Kluge 1966, Estes 1970, Brown 1976). Cope (1889) placed the American spadefoot toads in the family Scaphiopodidae and divided the species into two genera as follows: *Scaphiopus* (*holbrookii* and *couchii*), *Spea* (*hammondii* with three subspecies, *hammondii*, *bombifrons*, and *intermontana*, and *multiplicata* as a species).

The genus *Scaphiopus* has a range from the eastern United States west to the Great Plains (Dakotas south to Texas). The exception is *couchii*, with a range west from southern Texas through the low desert valleys of southern New Mexico, southern Arizona, and into southwestern California between Needles and Vidal Junction (Tinkham 1962). The range also includes northern Mexico from Tamaulipas to Baja California.

The genus *Spea* occurs in the western United States from the Great Plains west to California and south throughout western and southern Mexico. At present four species are listed for this genus (*bombifrons*, *intermontana*, *hammondii*, and *multiplicatus*) (Brown 1976). There is, however, some question as to whether all are valid as species. This is discussed further below with a brief review of the history of the genus *Spea*. The genus *Spea* was established by Cope (1875) to include the species *stagnalis* from northwestern New Mexico. In this report Cope also proposed the family Scaphiopodidae and included the species *bombifrons* in the genus *Spea*. In 1889 he listed *Spea hammondii* and included *bombifrons* and *intermontana* as *hammondii* subspecies; species status was retained for *multiplicata*.

Cope (1889) gave the following description for the genus *Spea:* "Cranial derm free from cranium; the latter generally with a frontoparietal fontanelle; vomerine teeth present; toes webbed; cuneiform process large." Recognizing that skull modifications had occurred in the genus, he stated: "In one of the subspecies of *S. hammondii* the ossification of the cranium has progressed so far as to close the frontoparietal fontanelle, but not so as to penetrate the cranial integument." Based on our present knowledge of the skull characters in *Spea* we can assume that Cope may have been referring to *intermontana*. Although Cope did not figure the skulls of the species he included in *Spea*, his descriptions strongly indicate that he recognized the uniqueness of the cranial characters, particularly the presence of a frontoparietal fontanelle. The latter is not present in the genus *Scaphiopus*.

Tanner (1939) examined specimens of the subgenus *Scaphiopus* (*holbrookii*, Massachusetts to Florida; *hurterii*, Benton and Lytle, Texas; *couchii*, San Pedro, Baja California; Waco, Fairbanks, and San Antonio, Texas; San Xavier Mission, Arizona) and figured a representative of each species (Fig. 11). The subgenus *Spea* was examined (*bombifrons:* Goodnight, Texas; Lexington, Oklahoma; Elkhart, Kansas; *intermontanus:* Carbon County, Garfield County, Kane County, Juab County, Uintah County, Washington County, Utah; *hammondii:* Cochise County, Arizona; San Jacinto, Riverside County, and San Diego, California; Ojos Negros and Punta Banda, Baja California) and skulls representing each taxon were figured (Fig. 11 reproduced from Tanner 1939, Plate I). He regarded each taxon as a species, in contrast to Cope (1889), who assigned them subspecies status. Schmidt (1953) accepted *bombifrons* and *hammondii* as species but placed *intermontana* as a subspecies of *hammondii*.

The dorsal skull figures of Tanner (1939) clearly illustrate the differences between *Scaphiopus* and *Spea*. It is difficult to assume that such structures should be considered as belonging within a single generic group.

In *Scaphiopus* there is a bony plate extending from the parietal area to the nasal. It covers the interorbital area and is suggestive of a primitive dermal plate. Whether it is a retained primitive dermal bone or one more recently developed, it is a unique, but uniformly simple, covering for the interorbital area. The interorbital skeletal structures in *Spea* are not readily comparable to those of *Scaphiopus*.

Zwiefel (1956) retained *Spea* as a subgenus within *Scaphiopus* and recognized Pelobatidae rather than Scaphiopodidae. His figures of the skulls vary little from those of Tanner (1939), and the relationship of the skin (derm) to the cranium was not considered. The study by Zwiefel (1956) provided an abundance of

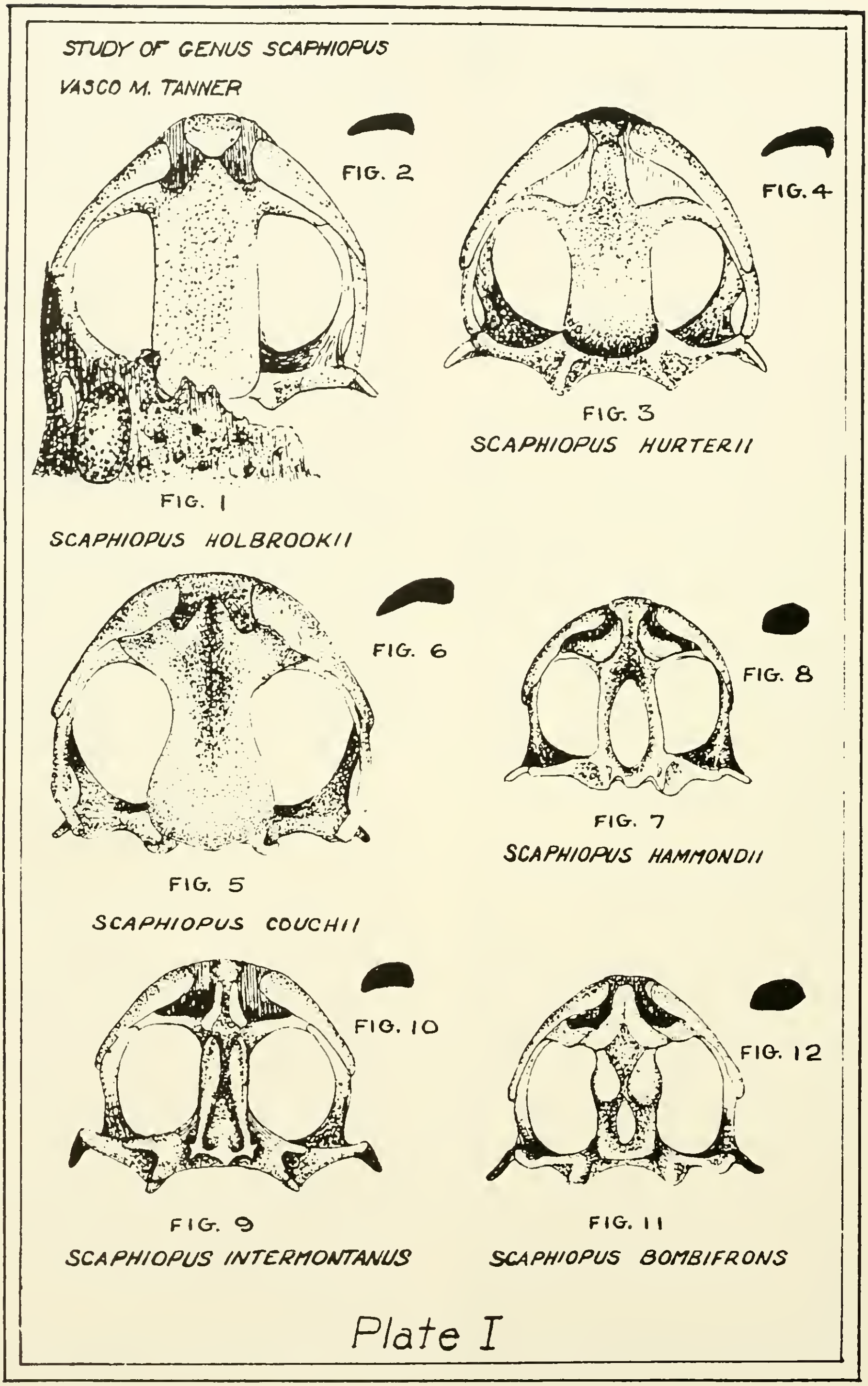
STUDY OF GENUS SCAPHIOPUS
VASCO M. TANNER
FIG. 2
FIG. 4
FIG. 1
SCAPHIOPUS HOLBROOKII
FIG. 3
SCAPHIOPUS HURTERII
FIG. 6
FIG. 8
FIG. 5
SCAPHIOPUS COUCHII
FIG. 7
SCAPHIOPUS HAMMONDII
FIG. 10
FIG. 12
FIG. 9
SCAPHIOPUS INTERMONTANUS
FIG. 11
SCAPHIOPUS BOMBIFRONS
Plate I

Fig. 11. Representative skulls of the genera *Spea* and *Scaphiopus* as prepared by V. M. Tanner (1939).

data; my only concern is that cranial characters were not adequately weighted when generic values were considered.

It is not only skull characters that vary, but also external characters such as the shape of the spade, smaller body size (S-V length), color pattern, and perhaps area of distribution. It appears that *Spea* is a western and southern group, whereas *Scaphiopus* is an eastern genus, in which *couchi* has more recently extended its range west to overlap that of *S. bombifrons* in the Great Plains and *hammondii* in Texas and west to California, including the adjoining border states of Mexico.

Cope (1889) in his key separated *Scaphiopus* from *Spea* on the character of derm involved in the cephalic ossification, which in *Spea* is "distinct from cranium, which is usually only ossified superiorly in two superciliary bars." Restated, the interorbital area is completely ossified in *Scaphiopus* (Fig. 11), whereas in *Spea* only bars of bone and an interorbital fontanelle provide little surface for the derm to be ossified with or to the cranium.

In recent studies other distinguishing characters have been established. Kluge (1966) summarized, in his Table 5, 17 diagnostic characters that distinguish the genus *Spea* from the genus *Scaphiopus*. To retain *Spea* as a subgenus in the genus *Scaphiopus* does not seem to be justified. I am persuaded to recognize *Spea* (as did Cope originally and Tihen [1960]) as a full genus based primarily on the distinct differences in the skull characters. Other characters as indicated by Kluge (1966) do not distract from such a taxonomic change.

Key to the Genera

1. Frontoparietal and nasal bones broad and complete, no interorbital fontanelle; derm ossified and adhering to cranium in the interorbital area; large, S-V length of adults 50+ mm; area between orbits wide, 5–7 mm; spade sickle-shaped and long .... *Scaphiopus* Holbrook

— Frontoparietal area with narrow bars between the orbits, separated by an interorbital fontanelle in *hammondii* and *bombifrons* but thin bone may extend between the interorbitals in *intermontanas;* smaller, S-V of adults 50 mm or less; area between orbits narrow, 4–5 mm; spade not sickle-shaped .... *Spea* Cope

Genus *Scaphiopus* Holbrook

Scaphiopus couchii Baird
Desert Spadefoot

Scaphiopus couchii Baird, 1854, Proc. Acad. Nat. Sci. Philadelphia 7: 62.

Scaphiopus couchii: Wasserman, 1970, Cat. Amer. Amph. and Rept. 85: 1.

Near Cd. Chihuahua, 5 (BYU 10440–44).

Colonia Dublan, 5 (BYU 2142–46i, 2771).

13 mi E Rancho Flores Magon, 4 (BYU 13967–70).

Colonia Juárez, 2 (BYU 14522, 15321).

Southern edge of Cd. Chihuahua, 4 (BYU 10424–27).

2 mi SE Colonia Juárez, 6 (BYU 13446–48, 15452–53, 15586, 15839).

Along road (Hwy 10) 15–30 mi SE Nuevo Casas Grandes, 33 (BYU 14075–14107).

12 mi S Samalayuca, 1 (UAZ 7671).

5 mi SE Galeana, 9 (UAZ 36428–36).

1.6 mi N Galeana, 7 (UAZ 34457–63).

7.1 mi N Cd. Chihuahua, 1 (UAZ 34458).

1.1 mi SW Nuevo Casas Grandes, 1 (UAZ 34456).

1.9 mi S Buenaventura, 2 (UAZ 36427, 36431).

5 mi N Cerro Campana, 17 (MVZ 68776–80, 70608–620).

7 mi N 3 mi E Cerro Campana, 5 (MVZ 70603–7).

Ojo de Laguna 1, (MVZ 12778).

29 mi W Gallego, 7 (MVZ 70600–2, 72776–7, 72779–80).

In the late afternoon of August 1957, Dr. Gerald Robison and I left Ciudad Chihuahua for Colonia Juárez. We intended to do night collecting along the road. Soon after dark a light rain began, and by the time we reached Sueco we were in heavy rain. We saw a few anurans on the road and noted an increase as we drove toward Rancho Magon. The heavy rain continued, and the numbers of anurans on the road increased. By the time we reached Galeana and crossed the Río Santa María, the desert was literally alive with frogs and toads. What had been a few days before a dry, barren landscape was suddenly an expanse teeming with thousands of croaking, hopping creatures that had literally erupted from the earth. Indeed, this was a "show time" not often seen, and, at this time, *Scaphiopus* was a primary participant (Fig. 15).

As we stood on the road and witnessed this assemblage of energetic creatures, we realized that only yesterday they were in a burrow and had perhaps been there for months or even a year awaiting this, their day, to fulfill their biological role in life's program. What a remarkable phenomenon.

Genus *Spea* Cope

A reexamination of the skulls as figured by Tanner (1939) and Zwiefel (1956) and the preparation of others from localities in the range of *S. hammondii* indicate that the latter is a polytypic species with at least three subspecies. The following key, which uses skull characters to separate the species in the genus *Spea*, will serve to identify the species.

Key to the Species of the Genus *Spea*

1. Frontoparietal bones narrow, ridgelike, unmodified and separated by a large fontanelle .... *hammondii*

— Frontoparietal bones modified by a boss or increased bony tissue reducing or nearly eliminating the frontoparietal fontanelle 2

2(1). An enlarged boss near anterior ends of frontoparietals, producing an external swelling between eyes; fontanelle small and posterior to bosses; skin smooth with few tubercles; body length of adults 45–55 mm .... *bombifrons*

— Frontoparietals enlarged ridges but without a distinct boss, fontanelle eliminated or greatly reduced by thin bone between ridges of frontoparietals; skin more rugose; body length of adults 50–60 mm .... *intermontana*

Spea bombifrons Cope
Plains Spadefoot

Scaphiopus bombifrons Cope, 1863, Proc. Acad. Nat. Sci. Philadelphia 15: 53.
Spea hammondii bombifrons: Cope, 1886, J. Acad. Philadelphia 2, 6: 81.
Spea bombifrons: Cope, 1889. U.S. Nat. Mus. Bull. 34: 5–525.
Colonia Dublan, 1 (BYU 415).
Outskirts Cd. Chihuahua, 5 (BYU 10440–44).
13 mi E Rancho Flores Magon, 5 (BYU 13962–66).

Neither Cope (1889), Kellogg (1932), nor Smith and Taylor (1948) listed this species for Mexico. Conant (1975) and Stebbins (1985) listed the range as extending from south central Canada through the plains of central U.S. and into northern Chihuahua. Firschein (1950) and Shannon (1953, 1957) listed specimens for Samalayuca and Cd. Chihuahua.

The existing records place this species in the lower valleys of north and central Chihuahua and not in the higher valleys such as Babicora or Madera just east of the Sierra Madre. In the higher valleys (7,000–9,000 ft) of the mountains only *multiplicata* was found.

Spea hammondii Baird
Western Spadefoot

Scaphiopus hammondii Baird, 1857 (1859). Explorations and Surveys for a Railroad Route from the Mississippi River to the Pacific Ocean 10, Pt. 4, No. 4: 12.
Spea hammondii: Cope, 1889. U.S. Nat. Mus. Bull. 34: 5–525.

There has been much uncertainty and doubt concerning the proper systematics for populations inhabiting a wide area in southwestern United States and Mexico. Brown (1976) included all populations of *Scaphiopus hammondii* that were east and south of California in a single species, *Scaphiopus multiplicatus*. His careful research of two populations (southern California and southeastern Arizona) added greatly to our understanding of life-history variables in these two segments of the *S. hammondii* complex. There are, however, two basic areas that are not yet fully researched. Apparently, there is little or no difference in the skeletal characters, and the two populations are interfertile with no apparent postmating isolation (Brown 1976: 2).

If we accept the skull characters as being the basic characteristic of the species in the genus *Spea* (as has been done for *bombifrons* and *intermontana*), then the open, unmodified frontoparietal fontanelle (Fig. 11 from Tanner 1939, his Fig. 7) is the basic character for the species *S. hammondii*. It is obvious that isolation and habitat modification were brought about by the desiccation after the Pleistocene period (Morafka 1988). External characteristics of the habitat were modified, of course, and then these variations directly affected the life-history characters of the populations in a wide area originally occupied by this species.

It seems reasonable to believe that in this widespread *hammondii* complex of populations there is a series of geographical subspecies that are related through cranial characters but show subspecific variations in external characters and life-history variables. Those who have examined the skulls (Tanner 1939, Zweifel 1956) have found no significant differences. The various populations show variation in the external anatomy (size S-V, skin texture, nature of mating calls, and adaptation to changes in the aquatic environment; Bragg 1945, Brown 1976).

The dorsal view of skulls from numerous localities indicates rather uniform skull characters for populations ranging over a wide area in southwestern United States and northwestern Mexico (Figs. 11, 12, 14).

The following key is an attempt to identify the subspecies that may presently be recognized. It should be noted that far more research dealing with all internal and external

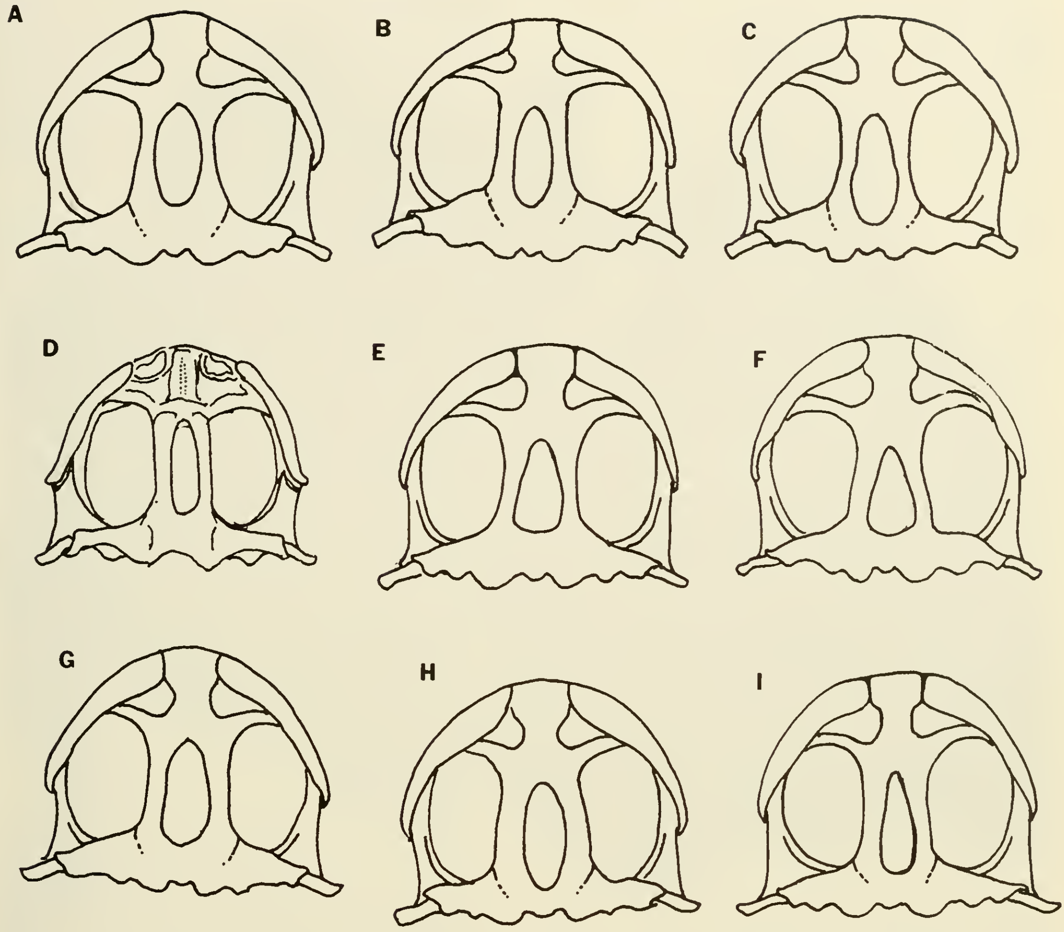

Fig. 12. Dorsal view of the skulls of *Spea hammondii* representing the following populations: A, Brewster County, Texas (BYU 2767); B, 0.5 mi W Kirtland, San Juan County, New Mexico (UNM 47614); C, Chiricahua Mt., Cochise County, Arizona (BYU 8932); D, Navajoland, Many Farms, Apache County, Arizona (LACM 127298); E, 11.1 mi NW Yepomera, Chihuahua (UAZ 34818, see Fig. 14A); F, 3.8 mi SE Yepomera, Chihuahua (UAZ 34814, see Fig. 14B); G, 18.8 mi N Cd. Durango (BYU 15526); H, El Rosario, Baja California, (BYU 34551); I, San Diego, California (BYU 2141). Note: These drawings are designed to show the size, shape, and position of the frontoparietal fontanelle to the dorsal skull structure in the species *Spea hammondii* Baird. These figures were prepared by Kaye H. Thorne.

characters must be done before a complete understanding of *S. hammondii* is obtained, particularly for the Mexican populations.

Key to the Subspecies of *Spea hammondii* Baird

1. Skin of upper parts unusually warty, dorsal tubercles large and numerous; heel usually reaching to tympanum (Fig. 13-A) ..... *h. multiplicata*

— Skin smooth or with fewer low tubercles; often a dorsal pattern of lighter stripes or spots; heel usually not reaching tympanum (Fig. 13-B) 2

2(1). Adults large, 50–55 mm S-V; interorbital fontanelle large and usually extending medially beyond the posterior margins of the orbits .... *h. hammondii*

— Adults smaller, 45–50 mm S-V; interorbital fontanelle large, but not extending posterior to the orbits .... *hammondii stagnalis*

REMARKS.—Differences in mating calls and adaptation to seasonal precipitation (March in California and July in Arizona) cannot be used as key characters for preserved museum specimens. Such life-history characters are important in demonstrating differences brought about by isolation and changes in the environment that have resulted from desiccation in an area of a formerly more widespread species. The data presented by Brown (1976) are important in that the biological evolutionary

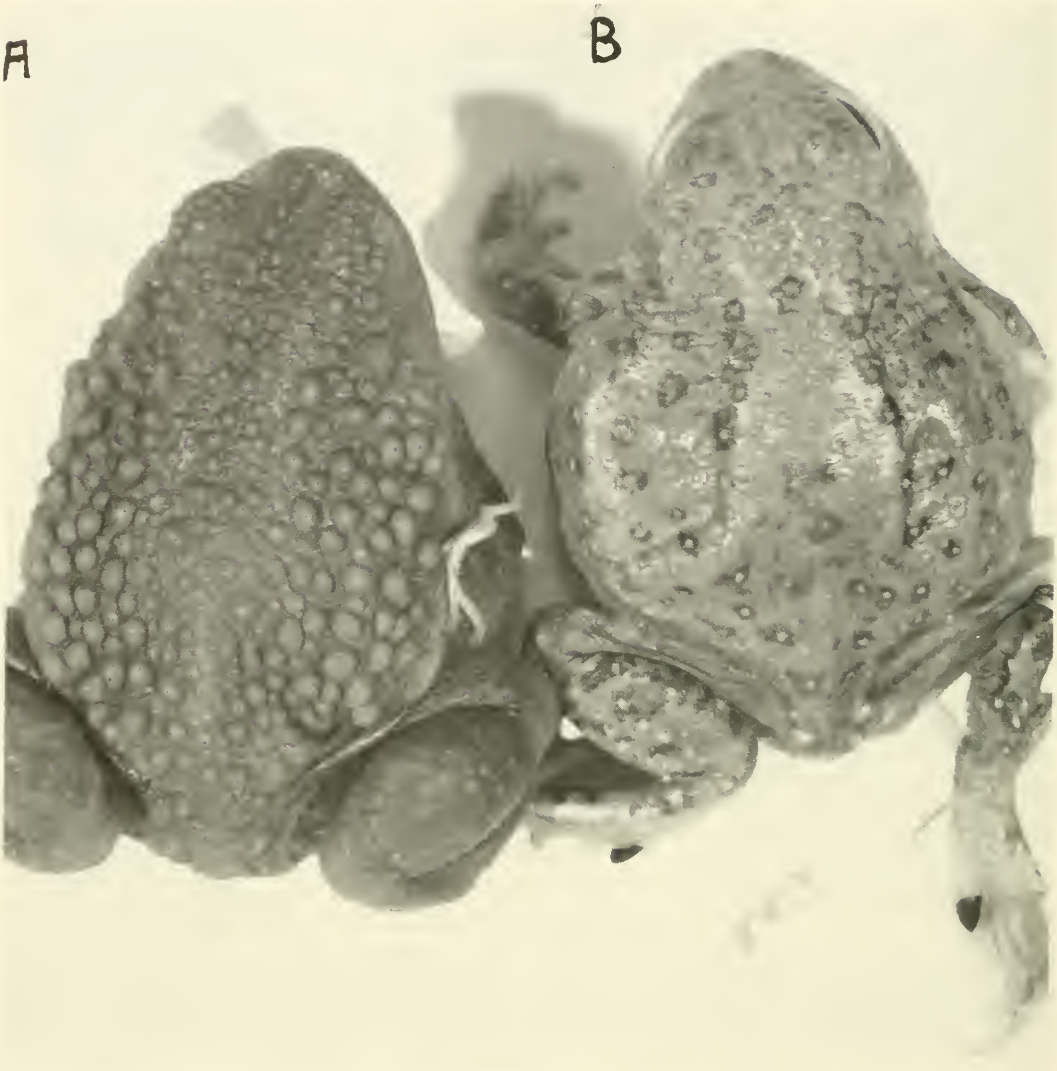

Fig. 13. *Scaphiopus hammondii:* A, *Spea h. multiplicatus*, UAZ 34818, 11.1 mi NW Yepomera, Chihuahua, on Road 16, ca 7,000 ft, in pine forest; B, *Spea h. hammondii*, UAZ 34814, 3.8 mi SE Yepomera, Chihuahua, on Road 16, ca 6,200 ft, in grassland; a distance of 15 mi and an elevation differential of 800 ft provide an environmental change that ecologically separates these populations.

divergence is established and provides population data that cannot be ascertained by a study of the external or internal anatomy. There are, however, few divergences in the crania of these widespread *hammondii* populations. They are apparently interfertile, although further research is needed for the extensive Mexican populations.

In view of the similarity in cranial characters and the fact that the widespread *hammondii* populations are interfertile, I am persuaded to consider *hammondii* a polytypic species, consisting of at least three subspecies: *h. hammondii* in California and Baja California; *h. stagnalis* in Arizona, New Mexico, southwestern Texas, and the valleys on each side of the Sierra Madre in Chihuahua, Durango, and Sonora. In the higher mountain valleys extending from western Chihuahua south into central and southern Mexico is *h. multiplicata*.

Spea hammondii stagnalis Cope

Scaphiopus hammondii Baird, 1859, Expl. Surv., R.R.

Miss. Pacific, 10, Pt. 4, No. 412. Fort Reading, California (part).

Spea stagnalis Cope, 1875, *in* Yarrow, U.S. Geol. Surv. W. 100th Meridian 5: 525. Northwestern New Mexico.

Scaphiopus hammondi hammondi Schmidt, 1953, Checklist North American Amphibians and Reptiles. Amer. Soc. Ichth. and Herpet. 6th ed., p. 59 (part).

Scaphiopus multiplicatus: Brown 1976. Los Angeles County Nat. Hist. Mus. 286: 1–15 (part).

12 mi SE Babicora (approx halfway between Babicora and Gomez Farias), 14 (BYU 14453–67, 15571–80).

10 mi W San Francisco del Oro, 1 (BYU 15677).

Chuhuichupa, 1 (BYU 15481).

0.3–18.3 mi SE Madera (along Hwy 16), 15 (UAZ 34649–51, 34656–61, 34663–64, 34666–68, 35040).

Yepomera 14 (UAZ 34652–55, 34804–13).

3.8 mi SE Yepomera, 1 (UAZ 34814).

6.2–6.6 mi NW Yepomera, 4 (UAZ 34815–17, 35041).

11.1 mi NW Yepomera, 1 (UAZ 34818).

2 mi S Santa Clara, 24 (MVZ 70622–70645).

1 mi S 1/2 mi E Santa Clara, 1 (MVZ 72790).

5 mi N Cerro Campana, 1 (MVZ 72791).

Ojo de Laguna, 1 (MVZ 72792).

Arroyo Mesteno (Sierra del Nido), 3 (MVZ 72787–9).

Specimens collected in the higher valleys (Babicora, Madera, and Yepomera) have fewer and lower tubercles and thus a smoother skin (Fig. 13). In other characteristics they do not vary greatly from specimens taken in the mountains. The relationships between those populations previously referred to as *hammondii* and *multiplicatus* show a close relationship but do show differences that suggest, at least in Chihuahua populations, that distinctions between mountain populations (7,000–9,000 ft) and those at lower elevations can be made on the basis of skin texture, if not on other characteristics (Fig. 13).

REMARKS.—In 1875 Cope described as a new species *Spea stagnalis*. The type locality is northwestern New Mexico on the Eocene Plateau. This population has been considered a part of the subspecies occurring in the lower southern valleys extending from southwest Texas west through southern New Mexico, Arizona, and the adjoining Mexican states of Chihuahua and Sonora.

The question arises as to whether *S. stagnalis* belongs to the southern populations or if indeed those populations in northern New Mexico belong to the northern species *S. intermontana* that have been listed as occurring in the Upper Colorado Basin and the Great Basin. An examination of the cotype USNM 25335 (that was figured by Cope 1875 in Yarrow, Plate 25, Figs. 6–8) determined that the cotypes had the same cranial characters as other populations in the *Spea hammondii* complex (Fig. 14). By recognizing the California populations as *Spea h. hammondii*, the eastern populations (Arizona, New Mexico, Texas, and those in the adjoining states of Mexico) must now be recognized as *Spea h. stagnalis* Cope.

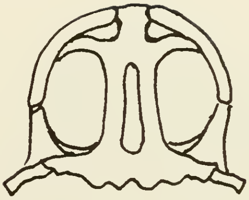

Fig. 14. *Spea stagnalis* Cope: cotype USNM 25335, northwest New Mexico, dorsal view of skull.

The distribution of the species of *Spea* is uncertain in the headwaters of the Río Grande and the Upper Colorado Basin. It appears that *bombifrons* extends well into the Upper Basin. A further study including populations in the adjoining areas north of *h. stagnalis* may provide a clarification of distribution as well as any further subspeciation that might have occurred in this rugged area consisting of mountains and plateaus dissected by deep canyons and isolated by deserts. To complete such a study is beyond the scope of this report. This report on the species *S. hammondii* is preliminary not only to an extensive study of this widespread species but also to a study of the entire genus *Spea*.

Spea hammondii multiplicata Cope
Mexican Spadefoot

Scaphiopus multiplicatus Cope, 1863, Proc. Acad. Nat. Sci. Philadelphia 15: 52.

Scaphiopus hammondii multiplicatus: Kellogg, 1932, U.S. Nat. Mus. Bull. 160: 22–24.

Scaphiopus multiplicatus: Smith and Taylor, 1948, U.S. Nat. Mus. Bull. 194: 36.

Chihuichupa, 35 (BYU 14388–403, 15391–409).

Cerocuhui, 2 (BYU 15502–3).

2 mi S Creel (along road to La Bufa), 6 (BYU 15598, 17801; UAZ 31220–23).

3.2 mi E Agostadero de Aguire, 1 (UAZ 46815).

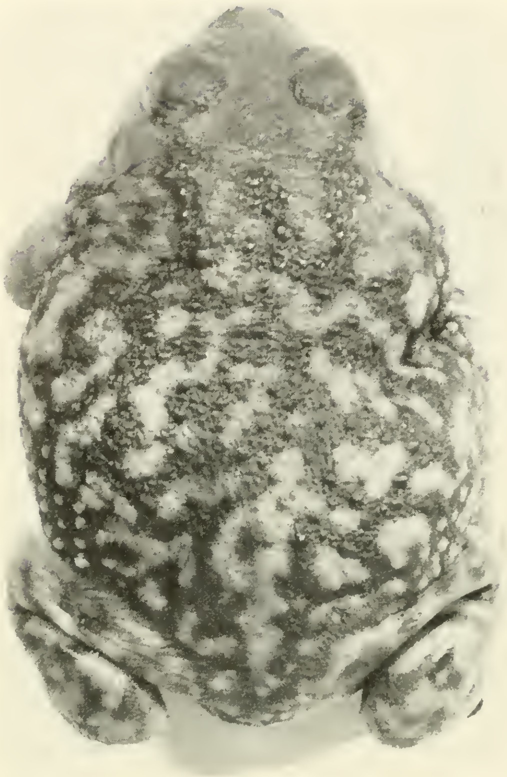

Fig. 15. *Scaphiopus couchi:* BYU 15839, collected 2 mi SE Colonia Juárez, 30 July 1958, S-V 69.5.

The distribution of *multiplicata* was considered by Smith and Taylor (1948) to be on "the plateau of central Mexico from Durango and Zacatecas southward." Conant (1975) did not recognize *multiplicata* and extended the range of *hammondii* to occupy not only southwestern United States but also the area previously designated for *multiplicata* by Smith and Taylor (1948). Stebbins (1985) apparently accepted the conclusions of Brown (1976) and replaced *hammondii* with *multiplicata* for essentially the same area indicated by Conant.

The relationship of these two taxa is close and thus warrants additional study. Until additional investigation establishes the degree of relationship, I will not attempt to further define the taxonomic status of the Mexican populations of *S. h. multiplicata*.

Family Bufonidae

Genus *Bufo* Laurenti

The state of Chihuahua contains nine species of *Bufo*. Some have entered the state from the north and east as a part of the desert habitat (*cognatus, debilis, punctatus, speciosus*, and *woodhousei*). Others occur in the mountains of the south (*simus*), the northwest (*microscaphus*), and the west (*marinus* and *mazatlanensis*).

Thus, this large state, with its eastern deserts, central foothills and low ranges, and western mountains and deep western canyons, provides a variety of habitats singular to Chihuahua. Within this diverse area is perhaps the largest assemblage of bufonid toads to be found in Mexico.

In this report no attempt is made to cite all the synonyms for these bufonid species. These can be found in the reports of Cope (1889), Kellogg (1932), or Smith and Taylor (1948).

Bufo cognatus Say
Great Plains Toad

Bufo cognatus Say, 1823, Long's Exped. Rocky Mts., Vol. 2: 190. Footnote: Arkansas River, Prowers County, Colorado.

Bufo dipternus Cope, 1879, Amer. Nat. 13: 437. Fort Benton, Choteau County, Montana.

Southern outskirts of Cd. Chihuahua, 4 (BYU 10457–60).

13 mi E Rancho Flores Magon, 7 (BYU 13955–61).
Approx 15 mi SE Nuevo Casas Grandes, 2 (BYU 14109, 15838).

25 mi SE Las Varas (Mennonite Village), 3 (BYU 15433–35).

Valley Road approx halfway between Babicora and Gómez Farías, 9 (BYU 15564–67, 15757–61).

Hidalgo del Parral, 6 adults and 21 untagged small ones (BYU 15558–63).

13.2 mi S Nuevo Casas Grandes, 2 (UAZ 34444–5).

4.9 mi N El Arco (36.5 mi S El Sueco), 2 (UAZ 34386, 34397).

2.0 mi N Villa Ahumada, 5 (UAZ 36281–2).

4.7 mi S Galeana, 2 (UAZ 36281–2).

1.0 mi NW Temosachic, 1 (UAZ 34832).

28 mi N Cd. Chihuahua, 1 (UAZ 34206).

3.7 mi S Buenaventura, 1 (UAZ 36280).

28 mi S Cd. Juaŕez, 1 (UAZ 34449).

5 mi N Cerro Campana, 6 (MVZ 70678–83).

Ojo de Laguna (25 mi S Gallego), 11 (MVZ 72764–80, 72784–7).

2 mi S Santa Clara, 4 (MVZ 70676–7, 72762–3).
Smith and Taylor (1948) list the following localities: Río Santa María near Progreso, near Villa Ahumada, 3 mi E Carmen and Colonia Juárez.

The above records indicate that the distribution of this species is in central Chihuahua primarily between the western mountains and eastern desert. Smith, Williams, and Moll (1963) report two specimens from Cuchillo Parada taken after a heavy rain. This locality is near the Río Conchos in northeastern Chihuahua.

Bufo debilis insidior (Girard)
Western Green Toad

Bufo debilis Girard, 1854, Proc. Acad. Nat. Sci. Philadelphia 7: 87.

Bufo debilis insidior: Smith, 1950, Misc. Publ. Univ. Kansas, Mus. Nat. Hist. 1: 75.

13 mi E Rancho Flores Magon, 7 (BYU 13948–54).

15–30 mi SE Nuevo Casas Grandes along Hwy 10, 6 (BYU 14108, 14110–14).

27.6 mi N Villa Ahumada (Hwy 45), 3 (UTEP 2059, UAZ 34830–1).

8.4 mi N Villa Ahumada, 1 (UAZ 11471).

3.9 mi N Villa Ahumada, 1 (UAZ 34472).

31.0 mi N Villa Ahumada, 1 (UAZ 34473).

2.0 mi N Villa Ahumada, 2 (UAZ 34828–9).

11.8 mi N El Arco Iris (31.3 mi S Sueco), 1 (UAZ 34471).

5 mi N Cerro Campana, 1 (MVZ 70647).

7 mi N 3 mi E Cerro Campana, 9 (MVZ 70648–56).

Ojo de Laguna, 10 (MVZ 72752–61).

During and immediately after heavy summer rains, this species may appear in great numbers along roads in Durango and Chihuahua. We collected 34 specimens 18.8 mi north of Durango City after a heavy evening rain on 24 July 1958 and could have collected a bushel from one roadside pond.

This species was unusually abundant, and we found ourselves in a community of toads and frogs the likes of which I had not seen before, but which I experienced again on the night of 28 July on our trip from Ciudad Chihuahua to Colonia Juárez. This species was seen along the road (Hwy. 45 and 10), at times in great numbers, but was particularly numerous in Chihuahua from Buenaventura to near Nuevo Casas Grandes.

I have followed Smith (1950), Schmidt (1953), and Conant (1975) in placing *insidior* as a subspecies of *debilis*. Determining whether there are two species, one east (*debilis*) and one west (*insidior*) as originally described by Girard (1854) and accepted by Smith and Taylor (1948), or whether this widespread group is indeed a series of subspecies must await an intensive study of the entire assemblage of available specimens. At present there is an abundance of material to be studied. This includes specimens from Zacatecas north through Durango, Chihuahua, Sonora, and into Arizona and New Mexico. The eastern segment extends from Tamaulipas north into Texas. A careful comparison of these populations may lead to an understanding of this interesting group of toads.

Kellogg (1932) lists two specimens (USNM 2622) from Chihuahua and notes the designation in the museum catalogue as the cotypes of *Bufo insidior*. No specific locality is listed in the catalogue, only Chihuahua, Mexico.

Bufo marinus Linnaeus
Giant Toad

Rana marina Linnaeus, 1758, Systema Naturae, Ed. 10, 1: 211.

Bufo horribilis Wiegmann, 1833, Isis von Oken 26: 654–655.

Bufo marinus Kellogg, 1932, U.S. Nat. Mus. Bull. 160-31-21, pp. 53–57, Fig. 11. Easteal 1986, p. 395.1–.4.

Urique, 10 (BYU 14355–64).

We arrived at Urique on the evening of 14 July and were soon greeted by large toads in the streets and along the nearby river. A moderate rain shower had occurred in the afternoon. Thus, it was warm and humid and we were soon aware that on such evenings toads and fruit bats were active. In the dim light of a nearby dwelling and from a radius of a few yards, 12 large toads were counted in less than one minute. As I moved about, their numbers did not seem to diminish. The next morning the toads were gone and were replaced by curious youngsters. Thus began three days in the old mining town of Urique.

Bufo punctatus Baird & Girard
Red-Spotted Toad

Bufo punctatus Baird & Girard, 1852, Proc. Acad. Nat. Sci. Philadelphia 6: 173.

36 mi S Ciudad Juárez, 1 (BYU 15207).

Ciudad Chihuahua, 1 (BYU 14252).

Cerocahui, 4 (BYU 14342, 14367, 14576–7).

Cuitaco, 3 (BYU 14527–29).

Urique, 1 (BYU 14341).

Crossing at Los Chales, 5 (BYU 15704–8).

35 mi SW Nuevo Casas Grandes, 1 (BYU 15454).

Colonia Juárez, 3 (BYU 17045–47).

Sierra del Nido Complex, 4.7 mi (by road) W Encinillas, 1 (UTEP 546).

7.5 mi (by road) ESE Buenaventura, 1 (UTEP 547).

NW La Junta at junction of road to Ciudad Guerrero, 1 (UTEP 558).
6.5 mi (by road) NE Ciudad Guerrero, 1 (UTEP 559).
Cd. Chihuahua, 1 (UAZ 11296).
Coyame, 5 (UAZ 34965–69).
8.3 mi W Coyame (hwy to Aldama), 1 (UAZ 34971).
11.2 mi W Coyame, 7 (UAZ 34972–78).
20.6 mi W Coyame, 1 (UAZ 34979).
15.0 mi S Nuevo Casas Grandes, 1 (UAZ 34470).
6.3 mi S Buenaventura, 4 (UAZ 36276–79).
6.5 mi NW Yepomera, 1 (UAZ 34826).
4.3 mi NW Yepomera, 1 (UAZ 34827).
2.7 mi S Milpillas (road to San Antonio, Sonora), 1 (UAZ).
24.6 mi S Ahumada, 7 (MVZ 52167–73).
Hidalgo del Parral, 1 (MVZ 58736).
5 mi N Cerro Campana, 18 (MVZ 68764–75, 70662–67).
2 mi S Santa Clara, 5 (MVZ 70657–61).

This species is seemingly widespread in Chihuahua, based on the above collection records. It should be noted here that much time was spent during the dry season when this species may not have been abroad. Our records place them in the desert valleys and foothill area usually between 5,000 and 7,000 ft in suitable habitats in central and western Chihuahua. We did not find them at the higher elevations.

Smith et al. (1963) report two specimens from eastern Chihuahua, one from near Beneficio and one from near Alamo. Both were near the Río Conchos.

Bufo speciosus Girard
Texas Toad

Bufo compactilis Wiegmann, 1833, Isis, p. 661 (part).
Bufo speciosus Girard, 1854, Proc. Acad. Nat. Sci. Philadelphia 7: 85–87.
Bufo compactilis speciosus: Smith, 1947, Herpetologica 4(1): 7–13.
Bufo speciosus: Conant, 1975, Field Guide: p. 313, map 268; Stebbins 1985, Field Guide: pp. 74–75, map 36.
1.7 mi NW Matachic, 1 (UAZ 34387).
2.5 mi NW Matachic, 1 (UAZ 34823).
2.6 mi SE Matachic, 2 (UAZ 34388–89).

The record for Guadalupe y Calvo may be in question. Webb and Baker (1984) collected *B. microscaphus* in this general area, and it is suspected that the Kellogg (1932) citation (USNM 47244) may be a confusion of *speciosus* (*compactilis*) with *microscaphus*. The latter is commonly found in the mountains, whereas *speciosus* is in the grassland plain habitat at lower elevations. Valleys in the general area of Matachic, Yepomera, and between Babicora and Gómez Farías are suitable habitats. Kellogg (1932) also listed *Bufo compactilis* for Colonia García, and Meadow Valley, where *Bufo microscaphus* occurs.

Stebbins (1985) did not recognize the records of Van Devender and Lowe (1977) for Matachic and confined the distribution of *speciosus* to a narrow edge of eastern Chihuahua. Conant (1975) extended the range into central Chihuahua, approaching the area of Matachic, but gave no locality records.

Originally, the valley between Gómez Farías and Babicora, to the northwest, was a grassy plain that served as a large cattle ranch. This may have been the case for other nearby valleys such as Matachic and Madera. In their original state these valleys seemingly served as havens for many species since they were at elevations above the hot, dry deserts and yet not in the mountains. On examination of the species listed in the report of Van Devender and Lowe (1977) one is impressed with the importance of this general habitat as a refugium as the deserts slowly claimed previous habitable areas after the last pluvial period.

Bufo microscaphus mexicanus Brocchi
Western Madre Toad

Bufo mexicanus Brocchi, 1879, Bull. Soc. Philom., Ser. 1, 3: 23–24.
Bufo microscaphus Cope, 1867, Proc. Acad. Nat. Sci. Philadelphia 18: 301.
Bufo woodhousii microscaphus Shannon, 1949, Bull Chicago Acad. Sci. 8(15): 301–12.
Bufo microscaphus mexicanus Webb, 1972, Herpetologica 28(1): 1–6.
Near Colonia Juárez, 2 (BYU 13516–17).
Chuhuichupa environs, 16 (BYU 13974, 14129–31, 14234–37, 14239–42, 15390, 15485).
Hope Valley at junction of Río Juárez, 1 (BYU 14238).
Mouth of Tinaja Canyon near Colonia Juárez, 1 (BYU 15581).
12 mi SE Babicora, 1 (BYU 15763).
Black Canyon, approx 8 mi W Chuhuichupa, 3 (BYU 14253–55).
26 mi W San Juanito, on road to Maguarichic, 1 (BYU 16957).
11 mi W San Juanito, 1 (BYU 16878).
San Juanito, 2 (BYU 15768, 17036).
2 mi SE Creel, 5 (BYU 15638–40, UAZ 37365–6).

25.5 mi S Creel, 2 (BYU 17048, 17050).
Cerocahui, 7 (BYU 14543–48, 14578).
Cuiteco, 3 (BYU 14294, 15507, 15781).
1 mi W La Laja, 1 (BYU 15872).
Maguarichic, 2 (BYU 16936–37).
Along Río Urique near Carmen Bridge, 9 (BYU 22703–22711).
Río San Miguel at San Juan de Dios, 1 (BYU 22623).
Río Gavilan, 1 mi SE Gavilanisto, 1 (UAZ 8960).
Basaseachic Parque Nacional, 2 (UAZ 47005, 47240).
Yaguirachic (130 mi W Cd. Chihuahua), 15 (MVZ 65982–93, 65996–8).

This is a widespread species in the western mountains of Chihuahua. It descends into the mouths of some canyons but has not been found in the desert valleys. The distribution of *mexicanus*, at least in Chihuahua, is apparently restricted to elevations at or above 6,000 ft. This is in contrast to *microscaphus*, which is found along desert streams in the southwestern United States (northwestern Arizona, and adjoining California, Nevada, and Utah) at much lower elevations. At none of the collecting localities were large numbers seen. The nine specimens taken near the Carmen Bridge were adults and juveniles.

Since *microscaphus* Cope (1867) and *mexicanus* Brocchii (1879) were described, various taxa have been used to include representatives of this species. Thus, for the past hundred years, populations of this species have been assigned as a part of *Bufo compactilis*, *Bufo columbiensis*, *Bufo woodhousei*, or as subspecies within one of the above or with a reference to such subspecies as *californicus* or *speciosus*. The close resemblance of *microscaphus* to other *Bufo* species in the southwestern United States and northwestern Mexico contributed to the taxonomic confusion.

Shannon (1949) recognized the distinctness of *microscaphus*, separated it from *compactilis*, but retained it as a subspecies of *Bufo woodhousei*. The detailed study by Webb (1972) has presumably extricated *microscaphus* from a confused and uncertain past and described it as a unique species, sharing similar characters with other sympatric species but with morphological characteristics such as uniqueness of foot tubercles, size, shape, and position of parotoid gland, warts on back low, rounded and mostly smooth, and color pattern of light brownish spots on the body and without spotting on the venter.

The nomenclatural review and description of *microscaphus* and its subspecies *mexicanus* by Webb (1972) has not only clarified the position of *microscaphus* and its subspecies but has also improved our understanding of its distribution in Mexico.

Bufo woodhousei australis Shannon & Lowe
Southwestern Woodhouse Toad

Bufo woodhousei Girard, 1854, Proc. Acad. Nat. Sci. Philadelphia 7: 86.
Bufo frontosus Cope, 1866, Proc. Acad. Nat. Sci. Philadelphia 18: 301.
Bufo woodhousei woodhousei Smith, 1934, Amer. Midl. Nat. 15: 449–57.
Bufo woodhousei australis Shannon & Lowe, 1955, Herpetologica 11: 185.

García, 1 (BYU 160).
Colonia Juárez, 2 (BYU 13581–2).
Colonia Dublan, 2 (BYU 13971, 15455).
Río Bavispe, below Tres Ríos, 2 (BYU 13458 and 13497).
Nuevo Casas Grandes, 1 (BYU 15455).
Yepomera, 1 (UTEP 2052).
2 mi N Yepomera, 1 (UAZ 34442).
6.3 mi NW Cd. Guerrero, 1 (UAZ 34443).
Yepomera, 12 (UAZ 34372–79, 34340–1, 34381, 34824).
6.9 mi NW Yepomera, 1 (UAZ 34645).
5 km N Yepomera, 1 (UAZ 36285).
2 mi SE Matachic, 2 (UAZ 12742, 34384–5).
Matachic, 1 (UAZ 34342).
4.5 mi SE Temosachic, 1 (UAZ 34382).
50 mi SE Galeana (Hwy 10), 1 (UAZ 34669).
2 mi N Janos, 3 (UAZ 34956, 36283–4).
6.5 mi N Nuevo Casas Grandes, (Hwy 10) 1 (UAZ 36286).
12.7 mi NW Gran Morales, 4 (MVZ 52179–82).
Río San Pedro, Meoqui, 2 (MVZ 52183–4).
Minaca (Río Papigochic), 5 (MVZ 52184, 58727–30).
Ojo de Laguna, 1 (MVZ 75873).
2 mi S Santa Clara, 8 (MVZ 70668–72, 70674–5, 72751).

The above records place this species in or near the Sierra Madre and north of the Río Papigochic. Conant 1974 (1977) extends its range southeast along the Río Grande and south along the Río Couchos into south central Chihuahua. *Bufo woodhousei* has been collected in streamside habitats and in the higher valleys near the western mountains where permanent streams are fed by springs. We did not find them in the mountains of western Chihuahua.

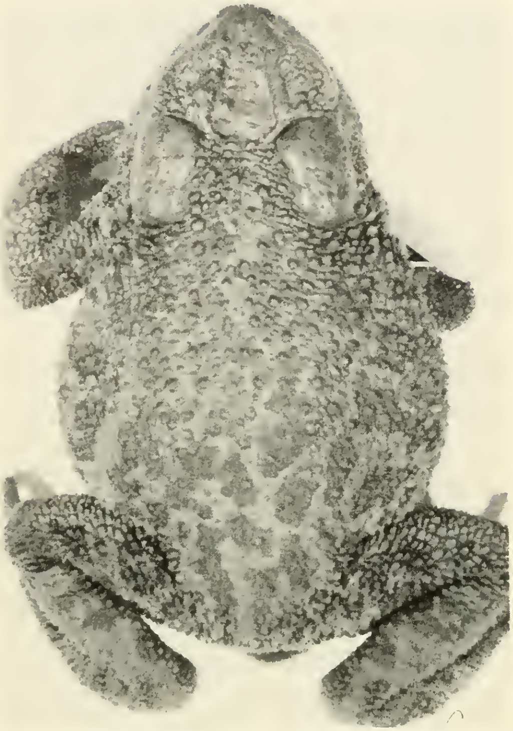

Fig. 16 *Bufo simus* Schmidt: BYU 17134, collected 25.5 mi S Creel, Chihuahua, 18 July 1960.

Bufo simus Schmidt

Bufo simus Schmidt, 1858, Denkschr, Akad. Wiss. Wien, math-nat. Class. 14: 254–55).

Bufo intermedius Gunther, 1858 (1859), Catalogue of the Batrachia Salientia in the collection of the British Museum, p. 140, pl. 9, Fig. FF.

Cerocahui, 1 (BYU 14542).
25.5 mi S Creel, 5 (BYU 17049, 17134–37).
SW Chihuahua, Río San Miguel, 1 (BYU 39373).

We found this species only in the Río El Fuerte basin and near streams during the rainy season. Smith and Taylor (1948) listed this species for Chihuahua but gave no localities. Webb and Baker (1984) did not report it for the Cerro Mohinora region during the dry season of late May (21–30). Its occurrence in adjoining Durango and Sinaloa suggests a distribution in the mountains of southern Chihuahua, at least southwest and southeast of Creel (Fig. 16).

Bufo mazatlanensis Taylor
Mazatlan Toad

Bufo mazatlanensis Taylor, 1939 (1940), Univ. Kansas Sci. Bull. 26: 492–494, p. 53, Fig. 1.

Urique, 14 (BYU 14343–54, 15556–7).
3 mi NNW Moris on Río Santa María (ca 800 m), Río Mayo drainage, 1 (UAZ).

This species was abundant along the Río Urique and in the streets of Urique on the evening of 14 July 1958. We were at Urique for three nights and two and one-half days. Between rain showers we collected specimens and tried to sample as many habitats as possible. It was at Urique that we first witnessed the emergence of multitudes of *Bufo* at dusk each evening.

While we were at Urique, the weather was hot and humid. Mornings were clear, but light rain showers occurred in the afternoons, contributing to the humidity and providing a proper environment for the toads each evening.

Family Leptodactylidae

Genus *Eleutherodactylus* Dumeril & Bibron
Eleutherodactylus tarahumaraensis Taylor
Tarahumara Barking Frog

Eleutherodactylus tarahumaraensis Taylor, 1940, Copeia 1940: 250–253.

Eleutherodactylus augusti: Bogert and Oliver, 1945, Bull. Amer. Mus. Nat. Hist. 83: 405–6.

Eleutherodactylus tarahumaraensis: Zweifel, 1956, Amer. Mus. Novitates. No. 1813: 28–33.

2 mi E Cerocahui, 1 (BYU 14385).
Maguarichic, 1 (BYU 16926).
6 km WNW Ocampo, 3 (UAZ 24741–2 and 47237).
The type (EHT-HMS 13008) collected at Mojarachic by Irving Knobloch.
7 mi SW El Vergel (Lagunita), 1 (MVZ 58797).
Yaguirachic, 2 (MVZ 65974–5).

The specimen taken at Cerocahui was under a rock in a moist area. It was spotted green on the back, had larger feet and eyes than other frogs of similar size, and had a snout-vent length of 23.5 mm. The specimen from Maguarichic was taken two years later (1960) at the same time, 13 July, and is 30 mm in S-V (Fig. 17). Both specimens are juvenile, and in neither locality could we find other specimens. Both were collected at a moist hillside habitat with permanent water at least 1/2 mile away. It should be noted that during the rainy season seeps occur in hillside depressions.

The figure by Zweifel (1956) of a specimen from southern Chihuahua has essentially the same color pattern as the juveniles listed above. Spotting is more diffused or less patterned than appears to be the case for other

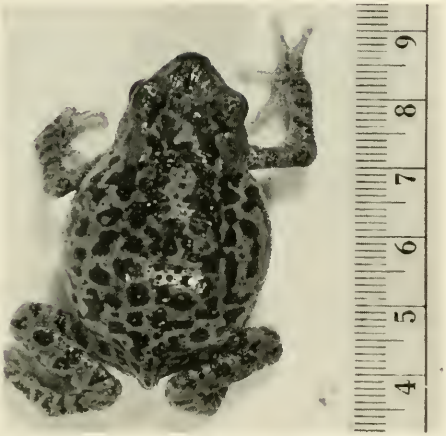

Fig. 17. *Eleutherodactylus tarahumaraensis* Taylor: BYU 16926, collected at Maguarichic, Chihuahua, 15 July 1960.

members of the *E. augusti* group. An intertympanic fold is not present.

In the eastern foothills of Sonora and Sinaloa, *E. augusti cactorum* Taylor occurs (Zweifel 1956). It is therefore to be expected in the low valleys of southwestern Chihuahua, as is the case for other species inhabiting the western foothills of the Sierra Madre and thus extending their distribution into the canyons of adjacent Chihuahua.

Family Hylidae

Genus *Hyla* Laurenti

Hyla eximia wrightorum Taylor

Arizona Tree Frog

Hyla eximia Baird, 1854, Proc. Acad. Nat. Sci. Philadelphia 7: 61.

Hyla gracilipes Cope, 1865, Proc. Acad. Nat. Sci. Philadelphia 17: 194.

Hyla wrightorum Taylor, 1939, Univ. Kansas Sci. Bull. 25: 436.

Hyla eximia wrightorum: Schmidt, 1953, A checklist N. Amer. Amph. and Rept., Amer. Soc. Ichthyologists and Herpetologists, p. 71.

3 mi N Chuhuichupa 19 (BYU 13800–1, 14512–17, 15411–12, 15482–84, 15728–29, 15733–36).

Black Canyon, 8 mi W Chuhuichupa, 5 (BYU 14549–53).

26 mi W San Juanito, on road to Maguarichic, 2 (BYU 16958–9).

1 mi W La Laja, 1 (BYU 16871).

1 mi SE Creel, 22 (BYU 15615–15636, 17078–9).

4 mi SE Creel, 2 (BYU 14518–19).

22.5 mi S Creel (La Bufa road), 1 (BYU 16946).

Cerocahui, 3 (BYU 15498–15500).

El Norte, 3 mi N Chuhuichupa, 7 (UAZ 35098–04).

1.4 mi SE Madera, 1 (UAZ 34469).

2.1 mi N Cuachochic, 1 (UAZ 46816).

Basaseachic, 1 (UAZ 46966).

Continental Divide, Sierra Verde, W of Casas Grandes, 1 (UAZ 13509).

In recognizing this taxon as a subspecies, I am following Schmidt (1953). An examination of the entire *eximia* complex may indicate full species status for *wrightorum*. This species distribution from Arizona to south central Mexico warrants careful study.

In the mountains of western Chihuahua this frog was observed at nearly all collecting stations during the rainy season. The ground color is green with a few round to oblong brown spots on the body. A brown stripe extends from snout through nostril to eye and from eye above the tympanum and terminating on body above the front legs. Hind legs have spots and reticulations. The largest specimen was 35 mm in snout-vent length, with most other adults at about 30 mm.

Hyla arenicolor Cope

Canyon Tree Toad

Hyla affinis Baird, 1854, Proc. Acad. Nat. Sci. Philadelphia 7: 61 (preoccupied by *Hyla affinis* Spix 1824).

Hyla arenicolor Cope, 1866, J. Acad. Nat. Sci. Philadelphia, Ser. 2, 6: 84. Type locality, northern Sonora.

Hyla copii Boulenger, 1887, Amer. Mag. Nat. Hist., Ser. 5, 20: 53.

Upper Fork Nutria Creek (near Chihuahua-Sonora line), 1 (BYU 13489).

Río Bavispe, below Tres Ríos, 3 (BYU 13434, 13445, 13449).

Chuhuichupa, 1 (BYU 15410).

Los Chales, 23 mi NE Tres Ríos, 1 (BYU 154703).

Along valley road approx halfway between Babicora and Gómez Farías, 9 (BYU 15494–97, 15501, 15568–70, and 14762).

1 mi W La Laja, 5 (BYU 16866–70).

Maguarichic, 5 (BYU 16931–35).

10 mi SW San Juanito, 1 (BYU 17080).

Cerocahui, 17 (BYU 14579–93).

2 mi SE Creel, 17 (BYU 15601–14, 15803–05).

22 mi S Creel, on road to La Bufo, 1 (BYU 16945).

Río Urique, near Carmen bridge, 40 mi SE Creel, 3 (BYU 31984–86).

Along Río Urique below Carmen Bridge 3–10 mi, 7 (BYU 22712–18).

Mouth of Arroyo del Creel at Río Urique, 1 (BYU 22720).

10 mi below Guachochic, 1 (BYU 22645).

10 mi above Pitahaya Pueblo on Río San Miguel, 3 (BYU 22639–41).

Río San Miguel near Tubares, 3 (BYU 22625–27).

Napuchic (ca 30 km N La Bufa), 5 (UAZ 31235–39).

2 mi S Creel, 11 (UAZ 31240–50).

6 mi E Yepomera, 3 (UAZ 34475–7).

11.2 mi NW Yepomera, 1 (UAZ 34481).

10.5 mi NW Yepomera, 1 (UAZ 34985).

Sierra del Nido, 1 (UAZ 42440).

0.7 mi N Loreto, 1 (UAZ 46613).

Basaseachic Parque Nacional, 1 (UAZ 46965).

This species is widespread in the mountains of western Chihuahua. We did not find it in the valleys east of the Sierra Madre except in the higher valleys such as the one southeast of Babicora and southwest in the general area of Yepomera.

In March of 1971, John Cross explored, by boat, the Río Urique from Arroyo Pamachic (SSW Creel) to Urique. The canyon for most of this distance is deep and in some places has sheer walls (see figures in Tanner 1985). In the mouths of some of the side canyons, or arroyos, are small side pools occupied by amphibians. Along the river, in small gravel and soil banks, are found the same types of vegetation as those present at Urique.

Family Ranidae

Genus *Rana* Linnaeus

Rana pipiens Schreber

Leopard Frog

Rana pipiens Schreber, 1782, Der Naturforscher 18: 185, pl. 4.

Colonia Dublan, 3 (BYU 301, 3657, 22115).

Río Bavispe (below Tres Ríos), 17 (BYU 13477–86, 13439, 13593, 14555–57, 14563–64).

Chuhuichupa, 7 (BYU 13947, 15724–27, 15731–32).

Upper Forks, Nutria Creek, 1 (BYU 13492).

14 mi SE Nuevo Casas Grandes, 9 (BYU 13374-80, 14127, 15456).

Cerocahui, 9 (BYU 14567–75).

Cuiteco, 5 (BYU 14530, 15662, 15775, 15779–80).

San Pedro, on Río Papigochic, 3 (BYU 14524–26).

Urique, 2 (BYU 14365–66).

Los Chales (23 mi NE Tres Ríos), 8 (BYU 15695–02).

2 mi SE Creel, 1 (BYU 15637).

Maguarichic, 7 (BYU 16938–44).

25.5 mi SE Creel (La Bufa Rd), 6 (BYU 17052, 17129–33).

Bocoyna, 1 (BYU 17097).

Springs at Guachochic, 5 (BYU 22648).

Basihuare, 1 (BYU 22702).

10 mi E Pitahaya Pueblo, 1 (BYU 22648).

SW Chihuahua Arroyo C. Prieta (Río Urique), 1 (BYU 22638).

8 mi N Basihuare, 2 (BYU 22633–34).

Barranca Colorado, 1 (Río Urique) (BYU 32267).

Head water Río Conchos (Rosabeachic), 4 (BYU 32010–13).

SW Chihuahua, Arroyo Damachic (Río Urique), 1 (BYU 39363).

SW Chihuahua, Arroyo San Canedaro (Río Urique), 1 (BYU 39372).

This is without a doubt the most widespread and common amphibian in the mountains of western Chihuahua. Webb and Baker (1984) report it from the Cerro Mohinora region, Smith et al. (1963) collected it from five localities along the Río Conchos (Julimes to Cuchillo Parado), and we saw individuals in a deep roadside pool on the north edge of Ciudad Camargo.

Three ranid species occur in Chihuahua. *Rana pipiens* is found throughout the state except in the desert valleys where aquatic habitats do not exist. However, they may be found at permanent springs that are isolated in desert valleys. *Rana tarahumarae* was found only in southwestern Chihuahua and the bullfrog along the Río Casas Grandes, at least from Rancho San Diego north.

I am making no attempt to specify a subspecies that may occur in the diverse *R. pipiens* assemblage. A comprehensive study to determine which subspecies occur is beyond the scope of this study. Until such a study is made, it appears best to list it as the *Rana pipiens* complex.

Rana tarahumarae Boulenger

Tarahumare Frog

Rana tarahumarae Boulenger, 1917, Amer. Mag. Nat. Hist., Ser. 8, 20: 416–17; Zweifel 1968: 66 1–2.

14 mi NE Cuiteco, 4 (BYU 15659–63).

25.5 mi S Creel (along La Bufa Rd), 2 (BYU 17115–16).

Maguarichic, 13 (BYU 16917–25, 16927–30).

SW Chihuahua, Arroyo Hondo (Río Urique), 1 (BYU 39371).

6 km WNW Ocampo, 3 (UAZ 47401–2, 47237).

Boulenger (1917) described this species from "several specimens, from Ioquiro and Barranca del Cobre, Sierra Tarahumare, N.W. Mexico . . . part of a collection presented by Dr. H. Gadow." In the collection of Dr. Irving W. Knobloch there were five specimens from Mojarachic.

This is a larger frog than *Rana pipiens* and appears to be more aquatic. We found specimens only along permanent streams and ponds, even during the rainy season in late July. Boulenger summarized the relationship of this frog as follows: "This species is very closely allied to *R. boylii*, differing in the larger eye, more oblique loreal region, the more distinct tympanum, shorter tibia and the absence of vocal sacs."

It appears that the isolation of *R. tarahumarae* in mountain refugia of the southwestern United States and northwestern Mexico is a direct result of the desiccation that occurred at the close of the Pleistocene period. As with other species that were widespread in the valleys of southwestern North America, these populations were slowly separated and isolated as the developing deserts restricted them to mountain habitats.

Rana catesbeiana Shaw
Bullfrog

Rana catesbeiana Shaw, 1802, Gen. Zool. 3: 106.

4.5 mi S Las Palomas, 3 (BYU 17011–13).

1.3 mi NW Nuevo Casas Grandes, 1 (UAZ 34468).

Bullfrogs were seen at the junction of Juarez Creek and Río Casas Grandes. This was a few miles north of Rancho San Diego. We also observed them around a pond 9.7 miles north of Meoqui. Conant (1974 [1977]) reports them along the lower Río Casas Grandes (6 miles north of Janos).

Family Microhylidae
Genus *Microhyla* Tschudi
Microhyla olivacea Hallowell
Great Plains Narrow-mouthed Toad

Engystoma olivaceum Hallowell, 1856 (1857), Proc. Acad. Nat. Sci. Philadelphia 8: 252.

Gastrophryne olivacea: Smith, 1933, Copeia 1933: 217.

Microhyla olivacea: Parker, 1934, Monograph of the Frogs of the Family Microhylidae 1934: 127–144.

Río Santa María, above the bridge on Hwy 10, 1 (BYU 15277).

Moris (west central Chihuahua), 2 (UAZ 46969 and 46972).

Smith and Taylor (1948) also report this species from the Río Santa María. Smith, Williams, and Moll (1963) collected four specimens from pools near the Río Conchos at Beneficio.

ACKNOWLEDGMENTS

Those individuals listed in the report entitled Lizards and Turtles of Western Chihuahua (Tanner 1987) were also involved in field studies or aided in providing additional data for this report. Their contributions, although not repeated, were important in assembling the specimens and data now at the M. L. Bean Life Science Museum (BYU).

I am indebted to Dr. Charles H. Lowe for the opportunity to examine the specimens from Chihuahua at the University of Arizona and to report the finding of *Pseudoeurycea belli* in Chihuahua. The University of Arizona collection (UAZ) added considerably to the number of specimens and species included and added to their distribution within Chihuahua. I am particularly grateful for the privilege of examining the adult salamanders that provided the necessary data to describe not only the larval stage but also the adults of *Ambystoma r. rosaceum.* I am also indebted to the following for locality data, loan of specimens, or geographical information: Mr. John L. Cross, who not only provided specimens but also aided in locality information for areas in the barrancas of southwestern Chihuahua; Drs. R. G. Webb and C. S. Lieb, who provided specimens and locality records for central and southern Chihuahua (UTEP); Dr. R. W. McDiarmid and Robert Reynolds, who loaned specimens from the U.S. National Museum (USNM); Dr. D. B. Wake, who loaned specimens from the University of California, Berkeley (MVZ); Dr. H. I. Snell, who loaned specimens from New Mexico (UNM); and J. W. Wright, Los Angeles County Museum (LACM), who loaned specimens.

Specimens were examined from the University of Illinois, University of Kansas, the U.S. National Museum, and the California Academy of Science. For these many opportunities, I am most grateful.

The photography was done by Mark A. Philbrick and Keith W. Judd. Karen Jensen and Terry Simmons did the typing and computer preparation, and the manuscript was reviewed by Drs. Hobart M. Smith and Charles H. Lowe. These courtesies and the support provided by the M. L. Bean Museum have aided greatly in the completion of the reports on the herpetological fauna of Chihuahua.

I am grateful to Dr. Irving W. Knobloch for data and information sent to me concerning his and Mrs. Knobloch's herpetological collections made primarily at Mojarachic and Maguarichic, but with other localities listed for Chihuahua. The first collections were made in the late 1930s (1939). These specimens were given to E. H. Taylor, who reported them in a conjoint paper in 1940. From this collection five new taxa were proposed by Taylor (1940, *Eleutherodactylus tarahumaraensis* and *Lampropeltis knoblochi;* 1941, *Ambystoma rosaceum* and *Ambystoma fluvinatum;* 1944, *Crotalus semicornutus*). There were at least 84 specimens in this collection that were added to the E. H. Taylor–H. M. Smith Collection. These specimens are at the University of Illinois (one-third) and Field Museum of Natural History (two-thirds).

Also among the data sheets are two additional collections. One made in 1954 contains 80 specimens collected at Maguarichic, Mojarachic, and a few from Texas; the second, made in 1957, contains 81 specimens from Chihuahua and Texas. These were apparently deposited at the University of Michigan. Letters from Norman Hartweg (1958) and Charles F. Walker (1962) list 29 species for the two collections. A list of 244 specimens (Knobloch No. 3901-4155), with some having the University of Michigan (UMMZ) catalog numbers (117755–117795), indicates that the larger part of the Knobloch collections is at the Michigan Museum. These collections consisted of: 9 species of amphibians, 1 turtle, 11 lizards, and 11 snakes, most of them collected in the mountains of west central Chihuahua, Mexico.

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OBSERVATIONS ON RECRUITMENT AND ECOLOGY OF RAZORBACK SUCKER: LOWER COLORADO RIVER, ARIZONA-CALIFORNIA-NEVADA

Paul C. Marsh[1] and W. L. Minckley[2]

ABSTRACT.—The Colorado River system downstream from Lake Mohave yielded 42 adult, 19 juvenile, and 39 larval wild razorback suckers (*Xyrauchen texanus*) between 1962 and 1988. Forty-six additional young captured between 1984 and 1987 may have been wild or stocked, hatchery-propagated fish. Wild juveniles of this endemic, imperiled species, with one exception, have not been otherwise known from the Colorado River basin downstream from the Grand Canyon since the 1950s. A majority of adults and larvae were from the river or its mainstream impoundments, while all but one wild juvenile and all presumably stocked fish were captured from irrigation canals. The ecology of artificial canals in which young razorback suckers survive and grow is poorly understood.

The razorback sucker, *Xyrauchen texanus* (Abbott), a once abundant endemic fish of the Colorado River basin of western North America, now occurs naturally in only a few places. Populations upstream from the Grand Canyon are small in size and apparently declining (McAda and Wydoski 1980, Tyus 1987, Lanigan and Tyus, in press). Downstream, a substantial remnant population persists only above Davis Dam in Lake Mohave, Arizona-Nevada (Fig. 1, Minckley 1983). That stock is comprised of old individuals (McCarthy and Minckley 1987), which despite annual reproduction have apparently failed to recruit for nearly four decades.

In the 1950s, and before, razorback suckers commonly occurred as a reproductive population in the Colorado River downstream from Davis Dam, in Lake Havasu, and below (Jonez et al. 1951, Douglas 1952, Jonez and Sumner 1954, Minckley 1983). They are presently rare or sporadic in those river reaches (Minckley 1979, Loudermilk and Ulmer 1985, Marsh and Minckley 1987); only a small number of adults and a few young fish have been taken in recent years (in part, Minckley 1983, Ulmer and Anderson 1985). Programs to reintroduce the razorback suckers into historic habitats have been initiated by the states of Arizona and California (Johnson 1985, Ulmer and Anderson 1985). Substantial stockings of hatchery-produced fish into the lower Colorado River mainstream were commenced in spring 1986, although a few experimental reintroductions were made earlier.

Occurrences of larvae or juveniles collected before the times of reintroductions, or in places inaccessible to stocked fish, represent natural production in the system. The intent of this paper is to separate records of natural occurrences from those attributable to hatchery fish. We document historic collections of small-sized razorback suckers downstream from Davis Dam, which, in light of recent age-and-growth and larval studies (McCarthy and Minckley 1987, Marsh and Papoulias, in press), provide evidence of recruitment to the population. We then report probable or known occurrences of reintroduced fish in the system; Langhorst (1988) further details short-term recaptures of hatchery-produced fish recently stocked by California. Comparisons of collection localities for juveniles before and following reintroduction efforts indicate that both wild and hatchery-propagated young of the species distribute themselves in similar ways, providing information pertinent to both the recovery program and the ecology of razorback suckers.

Acronyms used in the text for various agencies are as follows: AZGFD, Arizona Game and Fish Department; ASU, Arizona State University; CADFG, California Department of Fish and Game; NVDOW, Nevada Department of Wildlife; USBR, U.S. Bureau of Reclamation; and USFWS, U.S. Fish and Wildlife Service. Funding for this work was

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provided by USFWS, USBR, and ASU. We thank the many biologists working on the lower Colorado River (acknowledged in text) for information leading to this publication.

RAZORBACK SUCKERS IN THE LOWER COLORADO RIVER

Natural Occurrences, 1962–88

Razorback suckers (>50 cm total length [TL]) are presently common in Lake Mohave, Arizona-Nevada, and larvae of the species (<15 mm TL) are seasonally abundant. Size-groups between the larval and adult life stages are, however, essentially absent from collections, despite intense sampling. Adults comprised an average of ~25% of total fishes caught in annual trammel net samples between 1975 and 1988 (Minckley 1983, Minckley and Marsh, unpublished data). Larvae occupy the littoral zone of Lake Mohave (Bozek et al. 1984, Marsh and Langhorst 1988), where 10–100 or more can be attracted to a strong light in a few minutes at night (Langhorst and Marsh 1986). They rarely occur in open water of the reservoir; Langhorst and Marsh (1986) captured only a single specimen in 22 tow-net hours in 1985, although larvae were at the same time common in near-shore habitats. Four juvenile specimens (three preserved, 33 to 54 mm TL; ASU 11567 and 11568), collected by AZGFD personnel in July 1987 (T. Liles, AZGFD, personal communication), are the only naturally spawned juveniles recorded from Lake Mohave since the 1950s.

In marked contrast, except for a small resident population in Senator Wash Reservoir, California (Medel-Ulmer 1980, Ulmer 1987), there are confirmed records since 1962 for only 42 adult razorback suckers from the entire lower Colorado River mainstream and associated habitats downstream from Davis Dam (Fig. 1), despite intensive fisheries surveys in that area. Sixteen adults were from Lake Havasu proper: five averaging 56.9 cm TL were caught in 1962; four >50 cm TL were observed in 1975; three averaging 65.4 cm were electrofished in 1976; one (56.9 cm) was collected from the Bill Williams Arm of the reservoir in 1979; two (unmeasured) were caught by anglers in 1984 (Ulmer and Anderson 1985); and a single fish 50.6 cm TL was gill-netted in 1986 (M. Giusti, CADFG, personal communication). Riverine reaches yielded 23 individuals: 12, all >50 cm TL, but unmeasured, were taken by various means from Blythe, California, downstream to Imperial Reservoir from 1969 to 1985 (Ulmer and Anderson 1985); nine others, mostly >60 cm TL, were angled, electrofished, trammel-netted, or observed in the Needles-Topock Gorge reach from 1972 through 1985 (Minckley 1983, Ulmer and Anderson 1985); and two, 57.2 and 61.0 cm TL, were trammel-netted from Laughlin Lagoon, Nevada, an artificial backwater about 8 km below Davis Dam in 1986 (M. Burrell, NVDOW, personal communication). An additional three adults, ~50 cm TL, were caught from the Central Arizona Project (CAP) Granite Reef Aqueduct in October 1986 (USBR 1986), which began withdrawing water in 1983 from the Bill Williams Arm of Lake Havasu. Two of the last were 25+ years of age, as determined by otolith analysis (original data; following methodology of McCarthy and Minckley 1987), and thus originated from Lake Havasu. There are no indications that adult razorback suckers in the lowermost Colorado River are occurring less frequently in the 1980s than in the 1960s, which is likely a reflection of low adult mortality and individual longevity (to at least 44 years; McCarthy and Minckley 1987).

Larval razorback suckers are as rare as adults in the lower Colorado River downstream from Lake Mohave. None was found in shoreline surveys with bright light at night in Lake Havasu in 1988. Razorback suckers accounted for only 0.56% of 6,617 larval specimens caught in tow-net samples in Lake Havasu and upstream riverine reaches in 1985 and 1986 (Marsh and Papoulias, in press). Eight individuals were taken in 1985 and 29 in 1986. Although catch per unit effort varied between years and among stations, similar abundances were indicated in riverine and reservoir habitats, and no areas of larval concentration were evident (Marsh and Papoulias, in press). Two larval razorback suckers, ~15 mm TL, were also identified among 5,036 larval specimens from the CAP canal in 1987 (G. Mueller, USBR, personal communication).

Twenty-four juvenile razorback suckers, ~15 to 37.1 cm TL, fish of sizes not otherwise known from Lake Mohave or elsewhere in the

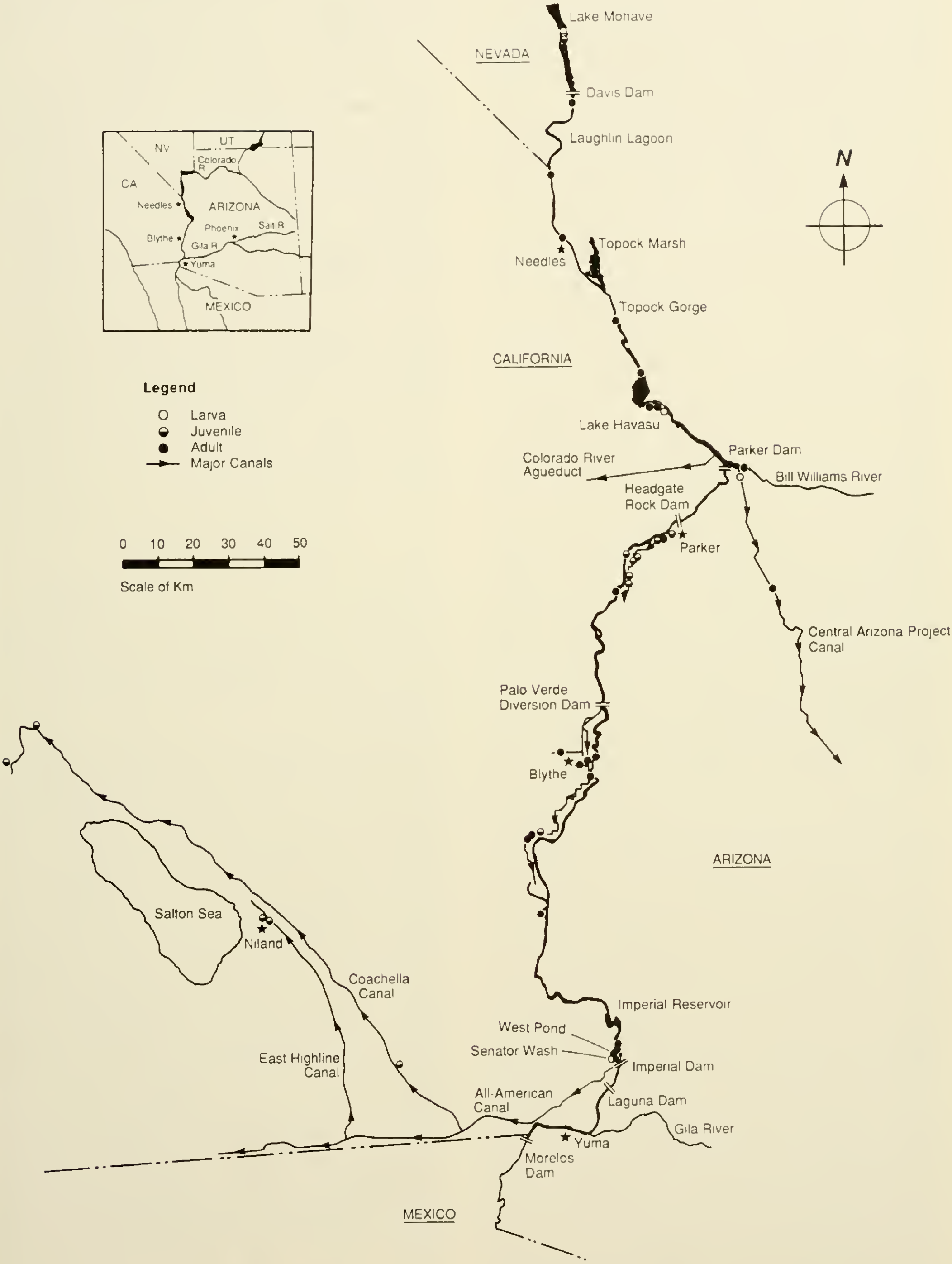
Lake Mohave
NEVADA
Davis Dam
Laughlin Lagoon
N
Needles
Topock Marsh
Topock Gorge
CALIFORNIA
Lake Havasu
Parker Dam
Colorado River Aqueduct
Bill Williams River
Headgate Rock Dam
Parker
Central Arizona Project Canal
Palo Verde Diversion Dam
Blythe
ARIZONA
Salton Sea
Niland
Coachella Canal
East Highline Canal
Imperial Reservoir
West Pond
Senator Wash
Imperial Dam
All-American Canal
Laguna Dam
Gila River
Yuma
Morelos Dam
MEXICO
NV
UT
Colorado R
CA
Needles
ARIZONA
Phoenix
Salt R
Blythe
Gila R
Yuma
MEXICO
Legend
○ Larva
◒ Juvenile
● Adult
Major Canals
0 10 20 30 40 50
Scale of Km

Fig. 1. Sketch map of the lower Colorado River, western North America, showing place names referred to in text and capture locations since 1962 for larval, juvenile, and adult razorback suckers.

Colorado River basin and thus the major subjects of this report, have been caught between 1974 and 1988 downstream from Lake Havasu. All but one were from the extensive system of artificial waterways that have been constructed for irrigated agriculture.

In Arizona, canals near Parker produced two fish (32.3 and 37.1 cm TL) in 1980, two specimens (each 30 cm) in 1981, and four averaging 35.2 cm in 1986 (Minckley 1983, Ulmer and Anderson 1985, S. Yess, USFWS, personal communication). Intake of water for the Parker area canal system is at Headgate Rock Dam, about 23 km downstream from Parker Dam. In California, one specimen (23.4 cm) was angled from a canal east of Palo Verde in 1983, which obtains its water from Palo Verde Diversion Dam, 21 km upstream from Blythe. Farther south, in Imperial Valley, the Coachella Canal (Fig. 1), its laterals, and its equalizing reservoirs produced three fish (average 34.8 cm TL) in 1984, and four others averaging 35.5 cm in April 1985 (Ulmer and Anderson 1985). Five young (~15 cm TL) were taken in 1973 and 1974 from the East Highline canal and adjacent ponds at Niland (St. Amant et al. 1974), a single fish measuring 22.5 cm fork length (FL × 1.085 ± 0.021 = 24.4 cm TL; unpublished data) was taken from the canal at Niland in 1974 (Ulmer and Anderson 1985), and another ~30.5 cm long was captured there from a canal-fed pond in December 1985 (E. Milstead, Niland, California, personal communication). Intake of water for the Imperial Valley is mostly through the All-American Canal, which originates near Imperial Dam (Fig. 1). The only small fish from the mainstem Colorado was a 35.1-cm individual captured 16 km downstream from Parker, Arizona, between Headgate Rock and Palo Verde Diversion dams, in summer 1987 (Langhorst 1988). That specimen was two years of age by otolith examination.

Assuming all these juvenile fish exhibited growth rates similar to those from Lake Mohave, hatchery ponds (McCarthy and Minckley 1987), and a variety of other waters where reintroduced populations have been studied (Marsh, in press, Marsh and Minckley, unpublished data), none was more than five years old. Only the eight fish captured in 1983 or later (three fish in 1984 and five others in 1985) from canals and other waters confluent with the All-American Canal (Fig. 1) could have been derived via West Pond from artificially propagated stocks (see below); all others were wild fish.

Reintroductions, 1980–88

The first razorback sucker reintroduction to the lower Colorado River area was in 1980. It consisted of 17 hatchery-produced adults (average 32.5 cm TL; 1974 year class, Toney 1974) and 3 Lake Mohave adults (average 56.6 cm TL, ages unknown) into the isolated West Pond, Imperial County, California (Fig. 1; W. Loudermilk, CADFG, personal communication). An unknown number of progeny of Senator Wash Reservoir fish, artificially propagated and reared by CADFG personnel, also were stocked in West Pond between 1981 and 1983 (L. Ulmer, CADFG, personal communication). In November 1983, 457 razorback sucker juveniles (average 95 mm TL) from Lake Mohave broodstock also were stocked into an artificial rearing enclosure constructed in West Pond by USBR; samples of those fish averaged 115 mm (N = 5) in December 1983 and 156 mm (N = 5) in January 1984 (Ulmer, personal communication). West Pond and the enclosure were not again monitored until 1988, when no razorback suckers were encountered.

Because water from West Pond is pumped into the All-American Canal, these stocked fish could have contributed to the eight post-1983 juvenile occurrences downstream in the confluent Coachella and East Highline canals or their adjacent ponds and reservoirs. Furthermore, progeny of Senator Wash Reservoir adults, artificially propagated in spring 1983, were also reared in aquaria in Blythe, California, and later transferred for grow-out in local ponds. A total of 57 survivors (average 28.5 cm TL for 39 measured) was stocked into the Colorado River mainstem near Blythe in April 1985 (Ulmer, personal communication). A dozen others (unmeasured) from the same group were stocked into an isolated pond on federal lands in February 1986 (Ulmer, personal communication). These last two stockings could not have contributed to subsequent captures from the areas of Parker, Arizona, or Palo Verde, California, because they were downstream from barriers created by Headgate Rock and Palo Verde Diversion dams (Fig. 1); however, fish could have made their way downstream to Imperial Valley.

The first major reintroduction of razorback suckers in the mainstream was in March 1986, when nearly 1.4 million larvae (10–18 mm TL) were released by CADFG and USFWS at various localities along the Colorado River from Devil's Elbow and Blankenship Bend (in the Topock Gorge area upstream from Lake Havasu, Fig. 1), downstream to Imperial National Wildlife Refuge near Yuma, Arizona. AZGFD and USFWS placed an additional 70,000 juveniles (~5.1 cm TL) into the Colorado River near Parker, Arizona, in May 1986, and CADFG stocked 4,163 juveniles (~20 cm TL) in the same area in October–November 1986. Since then, more than a million additional larvae and juveniles have been stocked downstream from Parker Dam (Langhorst 1988). These last stockings were all conducted later than the collections of all but one (Niland, December 1985) of the juveniles tabulated above, and of larvae reported by Marsh and Papoulias (in press).

Captures, 1987–88

Excluding the 1987 collection (Langhorst 1988) of a two-year-old individual in the Colorado River mainstream upstream from Palo Verde Diversion Dam (thus wild-hatched), a total of 41 juvenile razorback suckers was captured from canals downstream from Parker, Arizona, on the east (Arizona) side of the Colorado River in 1987 and 1988 (S. Yess, USFWS, personal communication). Thirty-eight fish caught in 1987 averaged 28.8 cm, and three taken in 1988 averaged 45.1 cm TL. Unfortunately, none from the first group was aged, but based on mean size they could have been one-year-old fish and therefore originated, at least in part, from the 1986 stockings. None could have been derived from earlier reintroductions, all of which were placed downstream from Headgate Rock Dam (Fig. 1). Fish of the second (1988) group had otolith ages of three, four, and seven years, having hatched, respectively, in spring 1981, 1984, and 1985. These were naturally produced wild fish, since dates of hatching do not correspond with those of any reintroductions in areas from which they could have moved to the collection sites.

DISCUSSION AND SUMMARY

Captures between 1974 and 1988 of at least 19 young, wild-hatched razorback suckers in the lowermost Colorado River system downstream from Lake Mohave provide convincing evidence of potential recruitment to that population. Numbers recruited nonetheless appear insufficient to maintain a population of adults, since fish of reproductive size are exceedingly rare and scattered in distribution (42 adult individuals recorded in the period 1962–1988). Further, artificial canals where most young fish were recorded may act not only as a refuge for early development but as death traps later, during annual dewatering for maintenance of the irrigation system. Because of this, potential recruits may ultimately be lost to the population.

Waterways of Colorado River irrigation systems consist of two major components, *canals* and *drains* (or *wasteways*). Canals vary downward from maximum flows of 400 m^3/sec. Water is withdrawn by gravity at diversion structures (e.g., Headgate Rock, Palo Verde, Imperial, and Laguna diversions) or through pumps (CAP and Colorado River Aqueduct intake facilities; USBR 1980; Fig. 1). Small *laterals*, which deliver water to agricultural fields or other points of use, are the least permanent, carrying water for only a few days or hours per month. Most canal habitats from which razorback suckers have been taken are of intermediate sizes that are dewatered at least annually for cleaning and repairs. Some of the largest canals may not be dewatered for periods of years.

Periodic cleaning and repair of canals is typically in the irrigation off-season, usually December or January. Fishes are decimated by dewatering and mechanical cleaning, and few survive (Marsh and Minckley 1982). However, razorback suckers spawn early, in late January through March, and larvae are thus available (generally from February through April; Marsh and Langhorst 1988) to colonize canals as they are placed back in service. Depleted populations of potential predators enhance larval survival, and razorback sucker growth rates (to 25+ cm in six months; unpublished data) are such that they rapidly grow out of predation range of small, abundant, nonnative predators (e.g., green sunfish, *Lepomis cyanellus*) and attain capabilities sufficient to avoid larger species (largemouth bass, *Micropterus salmoides*, and ictalurid catfishes, especially flathead catfish, *Pylodictis olivaris*). Further, annual drainage of canals makes young razorback suckers susceptible to collectors. Now that the species is known from such places, biologists are alert for their occurrence. Interest among biologists along the lower river and extensive information exchange stimulated by active reintroduction programs have contributed to and increased the probability that razorback suckers will be noted.

Drains transport excess water used for leaching of salts from agricultural lands back to the river. They are fed by over-surface flow during irrigation cycles and subsurface percolation the rest of the time, which results in slow-moving, enriched aquatic habitats that are often densely vegetated by algae and macrophytes and may be characterized by chemical and thermal extremes (Minckley 1979). Drains are far more permanent than canals. Large drains rarely dry and are only sporadically disturbed by cleaning and maintenance operations in ways, such as dredging, that do not involve dewatering. There are, however, no known records for razorback suckers from drains.

Origins of Recruits

Larvae are most likely passively entrained into canals. Currents at intakes are substantial, and larval razorback suckers tend to be near shorelines, at least in reservoirs (Langhorst and Marsh 1986) and also in the only historic collection of aggregated larvae and juveniles of the species recorded from the mainstream Colorado River in 1950 (R. R. Miller, in Sigler and Miller 1963). Drifting catostomid larvae (*Catostomus insignis, Pantosteus clarki*) in the Gila River, New Mexico, were concentrated by a factor of 6.5 near banks compared with samples in midstream (Bestgen et al. 1987). Reintroduced juvenile razorback suckers also show a marked proclivity to move downstream (Brooks 1985). Such behavior would obviously enhance the probability of encountering a withdrawal point.

The absence of razorback suckers in drains may result from a lack of sampling. As noted above, these habitats are far more permanent than canals. In addition, they are more complex, and thus exceedingly difficult to sample. Drains may also suffer seasonal chemical and physical extremes that are lethal to fishes. They nonetheless often support substantial populations of nonnative species (Minckley 1979, Matter et al. 1986), including centrarchids and ictalurids that are demonstrated predators on young razorback suckers (Osmundson 1987, Marsh and Brooks, in press). Drains furthermore flow into the river, and larval or juvenile razorback suckers may either not actively ascend against current or may be blocked from ascent by structures designed to prevent headward erosion.

Young razorback suckers in the lower Colorado River system may have hatched in a number of places. Downstream, the Senator Wash Reservoir population occupies a small (190 ha) pump-storage impoundment, where they behave similarly to fish in Lake Mohave. A small number of adults (estimated population 54 ± 22 individuals [95% confidence limits] in 1980–81, which averaged ~60 cm TL in 1973–74 [10 fish]) spawn and produce larvae each year, which then disappear before achieving juvenile size (Ulmer and Anderson 1985). Some of these could conceivably pass through penstocks of the reservoir and enter downstream intakes that lead to Imperial Valley canals. Fish appearing in the Parker, Arizona, and Blythe, California, areas could similarly originate from reproduction in Lake Havasu (Marsh and Papoulias, in press), pass through epilimnetic penstocks of Parker Dam, and then be diverted into canals at Headgate Rock Dam or Palo Verde Irrigation Diversion, respectively. Other spawning areas are unknown but certainly may exist (Loudermilk 1985).

Occurrence in the Parker, Arizona, area in 1987 of 38 juveniles of a size attributable to the 1986 reintroductions, and three in 1988 that were wild fish, underlines a number of needs and factors to consider. First, it is imperative that reintroduced fish be marked, by fin removal or with oxytetracycline, for example, so they may be certainly and readily discriminated from naturally produced individuals. Only in this way can the relative contributions of natural and reintroduction recruitment be evaluated. Second, assuming that some or all fish caught in 1987 were reintroduced, stocked and naturally produced larvae and juveniles must behave similarly, since they both appear to have passed from the river into canals. This provides information that razorback sucker larvae and/or juveniles drift or move downstream after hatching (or introduction), and likely did so in the natural state.

Last, survival to the juvenile stage in predator-poor habitat of canals further strengthens the hypothesis (Minckley 1983, Marsh and Langhorst 1988) that attributes lack of recruitment by this imperiled species to direct predation by introduced, nonnative piscivores.

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COMPETITION BETWEEN ADULT AND SEEDLING SHRUBS OF *AMBROSIA DUMOSA* IN THE MOJAVE DESERT, NEVADA

Richard Hunter[1]

ABSTRACT.—Seeds of the perennial shrub *Ambrosia dumosa* germinated in abundance following 11 days of rain during August 1983 at a study site in the northern Mojave Desert. Seedling establishment, growth, and reproduction were observed in natural vegetation and in an area that had been previously cleared of vegetation. For 5,527 *A. dumosa* seedlings, percent survival in April 1986 averaged 3% in the undisturbed vegetation and 58% in the denuded area. Seedlings occupying the cleared area had grown to sizes up to 0.1 m^3 by October 1984; some produced flowers and fruit in the spring of 1985. Surviving seedlings in the undisturbed vegetation were all smaller than 0.001 m^3 and did not reproduce. These pronounced differences in growth, survival, and reproduction associated with the presence or absence of adult shrubs demonstrated an intense competition that is incompatible with indications of mild competition from nearest-neighbor analyses. I therefore hypothesize that competition for water occurred, not by competition for water in two dimensions but by rapid use of a common resource, as if several people were drinking with straws from a common cup. This temporal mechanism would strongly favor adults over seedlings.

Attempts to detect the occurrence of "competition" in desert vegetation have depended largely on analyses of spacing and the distribution of shrub populations (reviewed recently by Fowler 1986, Ismail and Babikir 1986). Regular spacing has been taken to imply that competition has occurred in the past. However, neither pattern nor spacing with respect to neighbors has produced unequivocal evidence that competitive interactions have major effects in desert plant communities (Wallace and Romney 1972, Yeaton and Cody 1976, Ebert and McMaster 1981, Fonteyn and Mahall 1981, Phillips and MacMahon 1981, Wright 1982, Schlesinger and Jones 1984). Some workers have presented direct experimental evidence that competition for soil moisture occurred between desert shrubs by demonstrating that removal of shrubs resulted in statistically significant increases in the water potentials of remaining plants (Ehleringer 1984, Fonteyn and Mahall 1978, Robberecht et al. 1983). Though competition in deserts has thus been acceptably "proven," it would appear from these studies to be a minor process in shrub population dynamics producing subtle effects subject to considerable debate.

To assess the role of adult-seedling competition on seeding survival, growth, and reproduction, I compared seedling establishment in undisturbed vegetation with that in an adjacent area denuded of shrubs. Heavy rains in August 1983 over an area including several denuded areas resulted in germination of numerous seeds of the shrub *Ambrosia dumosa*, initiating the study.

STUDY SITE

The focus of the study was a 43 × 1,000-m area in Jackass Flats, Nevada (36°42'N, 116°24'W, 1,100 m altitude), cleared of vegetation by surface blading in 1979 (Major W. Jacobs, personal communication) for a purpose unrelated to this study. Prior to the *A. dumosa* germination, the denuded area supported a sparse population of the perennial grass *Oryzopsis hymenoides*. The abundant germination of *A. dumosa* appeared to be a highly localized event, extending approximately 1.3 km E, 3.3 km N, and 3–5 km S and W of the study site. The rain that caused germination fell almost daily 9–19 August 1983, totaling 99 mm at the nearest NOAA weather station 11 km away. That rainfall amount in such a short period was unprecedented in 23 years of record.

Soils in west Jackass Flats are sandy to a depth of at least 1 m (Romney et al. 1973, site 72). Natural plant cover consists largely of the shrubs *Larrea tridentata* and *A. dumosa*, together with sparse individuals of *Ceratoides lanata*, *Acamptopappus shockleyi*, and *O. hymenoides*.

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METHODS

In January 1984 a 100-m steel tape was laid at right angles to the long axis of the denuded area extending 25–32 m into undisturbed habitat on either side of the denuded plot. All seedlings were counted (but not measured) in a 1-m swath on one side of the tape. In addition, measurements were made of the heights, maximum widths, and the perpendicular widths of all mature shrubs (>10 cm in any dimension) and the grass *O. hymenoides* occurring in a 2-m swath centered on the tape. (The greater width was chosen to increase the number of individuals sampled for the sparser *O. hymenoides* and adults.) At subsequent censuses in October 1984, June 1985, and April 1986 all plants, seedling and adult, were measured and their reproductive states recorded. Seedlings that occurred in clusters were measured individually. The area covered by each shrub was calculated as an ellipse with the two radii equal to half of the two measured widths. Total cover was corrected for overlapping canopies. Shrub volume was estimated as the volume of an elliptical cylinder the height of the shrub.

RESULTS

In January 1984 seedling density of *Ambrosia dumosa* ranged from 0 to 535/m^2. In the undisturbed vegetated area the seedlings were quite uniform in size and appearance. Individuals ranged up to 3 cm tall and lacked branches and expanding leaves. In the disturbed area they were somewhat larger and vegetative. They bore short branches and healthy green leaves and appeared to be actively growing. All but three new *A. dumosa* on the denuded area were less than 10 cm in any dimension. Remains of cotyledons, some still green, were apparent.

There were 5,527 *A. dumosa* seedlings in the first census. At the same time there were 15 *Larrea tridentata* and 3 *Acamptopappus shockleyi* seedlings. Ten of the *L. tridentata* and all *A. shockleyi* seedlings occurred in the undisturbed area; none of these survived to June 1985. Three of the 5 *L. tridentata* that germinated on the denuded area survived. Along the 2-m-wide transect there occurred 43 *Oryzopsis hymenoides* seedlings in the undisturbed area, 17 of which survived to June 1985, and 9 in the denuded area, 5 of which survived. Cover by adult perennials in the undisturbed sections was by *A. dumosa* (10.5%), *L. tridentata* (7.1%), and other species (0.3%).

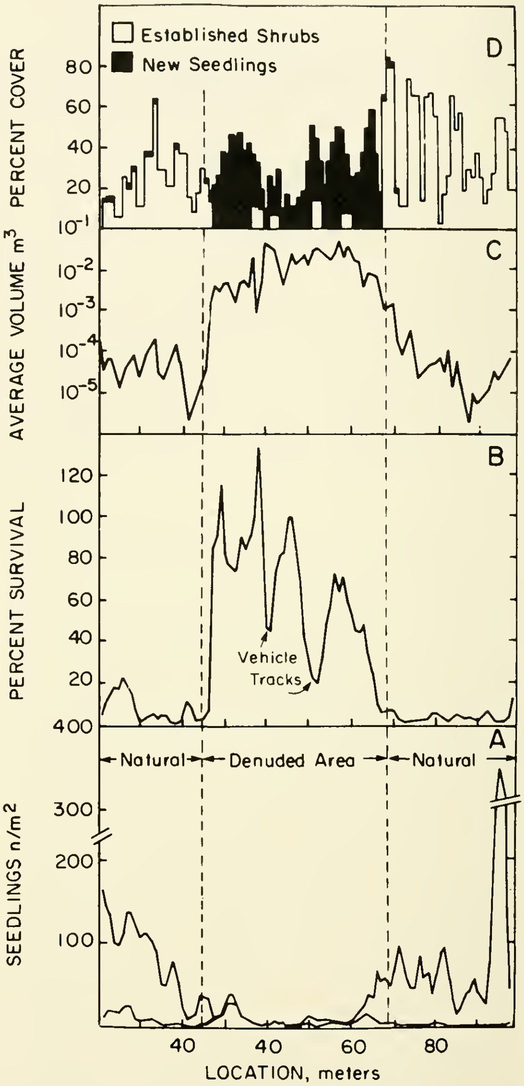

Fig. 1. Population characteristics of a cohort of *Ambrosia dumosa* seedlings spanning a 43-m-wide denuded area: A, density of seedlings in January and October 1984 (three meter moving average); B, percent survival in June 1985 (three meter moving average); C, average aboveground volumes; D, cover by seedlings and mature plants (*Larrea tridentata*, *A. dumosa*, and *Oryzopsis hymenoides*).

Ambrosia dumosa seedlings were more numerous in quadrats in the natural vegetation area than in quadrats located on the denuded area (Fig. 1A). They also were more dense on

TABLE 1. Logarithmic growth rates ($k = \ln(V2/V1)/dT$) and volume-doubling times (days) for *Ambrosia dumosa* seedlings and adults between September 1983 and October 1984.

Location (m)	Habitat	n	k ± sem	Doubling time
0–25	Control	21	3.5 ± 0.2	72
26–30	West edge, scraped	5	7.5 ± 0.2	34
29–63	Central scraped	27	8.6 ± 0.2	29
64–68	East edge, scraped	3	7.6 ± 0.6	33
69–99	Control	23	3.2 ± 0.3	79
0–99	Control adults	28	0.6 ± 0.1	420

the edges than in the center of the denuded area. Many occurred near or in obstructions, such as around the bases of *O. hymenoides* clumps, around standing dead wood, in shallow depressions where litter and seeds collected (Reichman 1984), or in small sand deposits in the lee of dead twigs lying on the surface.

Percent survival in June 1985 is plotted in Figure 1B. Survival near the center of the disturbed area reached 100% in some quadrats and averaged 65%, whereas in the natural vegetation it averaged only 5% ($X^2 = 1461$, 1 d.f., $p < .0005$). Survival on the disturbed area appeared to taper off near the edges (Fig. 1B). A decrease in survival between 48 and 55 m was due to infrequent vehicle traffic (over which I had no control) crossing the transect. (Survival exceeding 100% in Figure 1B arose from small counting errors at the initial census due to clustering of seedlings and slight variations in repositioning the steel tape.)

By October 1984 there was a striking difference in seedling size between the disturbed and undisturbed plots (Fig. 1C). Within 14 months of germination, individual plants in the center of the disturbed area had reached nearly 0.1 m^3 in canopy volume, while none in the natural vegetation exceeded even 0.001 m^3. Consequently, by October 1984 average cover on the disturbed area (26 ± 3%) exceeded cover in the natural vegetation of the undisturbed sections of the transect (18.6%) (Fig. 1D). In June 1985 and March 1986 cover was lower than in October 1984.

Logarithmic growth rates (Erickson 1976) were calculated for the period from germination to October 1974 (Table 1). They demonstrated what is visually apparent in Figure 1C: the growth of surviving seedlings was much slower in the control areas than on either the edges or center of the denuded strip.

Proportionally, growth of surviving seedlings in the control areas was more rapid than that of adults, but in absolute volume growth, adults (January–October 1984; 134 m^3/ha) far surpassed seedlings (germination–October 1984; 2.6 m^3/ha). Adult survival was 100% between January and October 1984, compared to 5% for seedlings.

In June 1985 there were 207 seedlings located between 31 and 62 m along the transect (the central denuded section), of which 31 had produced flowers and/or fruit. The mean volume of the reproductive plants was .031 m^3 (s.e. = .004), and the smallest was 0.0016 m^3. Slightly more than 50% (24 of 47) of the seedlings between 40 and 55 m flowered in 1985. All other seedlings along the entire transect remained nonreproductive.

DISCUSSION

Dominant shrub species in the Mojave Desert are long-lived (Johnson et al. 1975, Hunter et al. 1980, Vasek 1980), and turnover in established populations is correspondingly slow (Shreve and Hinckeley 1937, Beatley 1980, Hunter et al. 1980, Goldberg and Turner 1986). Storm-initiated germination and subsequent high seedling mortality are typical (Went and Westergaard 1953, Sheps 1973, Friedman and Orshan 1975, Ackerman 1979, Ebert and McMasters 1981), though the densities I observed were extreme. The excellent survival I found on the denuded area has not been previously reported.

Denuded areas in the Mojave Desert normally require many years to regain even a semblance of original cover and diversity (Vasek et al. 1975, Romney et al. 1980, Wallace et al. 1980, Webb and Wilshire 1980). The rapid restoration of cover by a dominant species is evidently unusual but concurs with observations of Shreve (1942).

There were bare patches in the vegetated area several meters in diameter associated with slight improvements in survival (6 and 98 m; Fig. 1B); yet growth was not improved in those patches (Fig. 1C). In contrast, at the edge of the denuded area growth increased dramatically within 1 m (Fig. 1C). In other words, there was relative uniformity of growth and survival within the two areas and a sharp divergence at the boundaries. In order to explain the uniformity, I postulate that soil moisture levels in each of the two areas were relatively uniform, and that the differences in moisture content were due to plant transpiration in the vegetated area. Thus, the apparently patchy shrubs resulted in uniformly dry soil.

I therefore propose, as a generalization, that in deserts, though shrub aboveground biomass is relatively patchy, soil moisture is relatively uniform. This could arise through rapid equilibration of soil water pools, depending on relatively rapid hydraulic conductivity through soils and roots (Richards and Caldwell 1987). It could also arise through uniform withdrawal of soil moisture by shrubs, but that mechanism is contradicted for wet soil by data of Cable (1977) and Fernandez and Caldwell (1975) on the spatial aspects of moisture withdrawal and root growth. Probably, as soil goes from wet (near 0 MPa) to dry (near 5.0 MPa), the mechanism producing uniformly available soil moisture would switch from equilibration by water movement to relatively uniform withdrawal by shrubs. Nevertheless, whatever the mechanism, this hypothesis relates significantly to current research on desert plant ecology, which attempts to infer competition by spatial analysis of aboveground biomass.

Went (1973), observing density-dependent growth of desert ephemerals, proposed that plants share rather than compete for resources, each individual growing in proportion to its share of the available resources. A less teleological view is that they had equal capabilities for resource utilization, thus making competition ineffective rather than absent. This is reasonable for desert ephemerals, which all start at a given time as seeds and then germinate and grow rapidly to maturity. My hypothesis is similar, except that it involves both adults and seedlings. It appears that though they shared a common pool of water, seedlings had a much greater probability of drought-induced mortality. They had less biomass to "store" water, smaller root systems, and were less self-shading. Their small size was, therefore, a probable cause of the differential mortality (see e.g. Cook 1979, Paine 1976, and Sebens 1982 on size-related mortality). The result was that adults utilized the majority of the resource, and, although seedlings grew proportionately faster than adults while water was available, they failed to become established because of their small size.

I offer no plausible alternative hypothesis to explain the large differences in growth and survival between seedling populations on and off the denuded site. Browsing damage was apparent on a few *A. dumosa* seedlings and on many *O. hymenoides*, but it was almost totally restricted to the denuded sections (Hunter 1987). The possibility of competition between seedlings did occur, but only on the denuded area, where seedling cover averaged 26 ± 3% (s.e.) in October 1984. In the vegetated areas, seedling cover was then only 0.7 ± 0.1%, while adult cover was 17.9% (Fig. 1D). To suggest that fertility or soil compaction might cause such major differences would be specious. Fertilizers have had little effect in the Mojave Desert without added water (Romney et al. 1978, Lajtha and Schlesinger 1986). There was no evidence of soil disturbance other than a slight compaction in the denuded area. Allelopathic interactions have been suggested for both *A. dumosa* (Muller 1953) and *L. tridentata* (Knipe and Herbel 1966), with some positive effects seen in the lab. But a study by Wallace and Romney (1972) showed positive association of *A. dumosa* with 17 species, *L. tridentata* with 12 species, and negative association with only 2 and 1 species, respectively. That, together with the improved growth of annuals under *A. dumosa* canopies (Muller 1953), implies that allelopathy is not significant in the field.

An analogy to my hypothesis is several people drinking a single soda, each with his own straw. The soda disappears at a rate proportional to the number of drinkers and their drinking rates, but independent of the distances between them. Similarly, my hypothesis suggests the evidence from spatial analyses for competition among desert shrubs is incomplete. Of what importance is distance between neighbors if root systems overlap, if soil water flows at significant rates, if a neighbor is orders of magnitude smaller, or has a different phenological pattern? I would argue that distance to the nearest neighbor is of minor importance. Of more relevance would be the sum of biomasses of neighboring plants, as in studies by Fowler (1984) and McAuliffe (1984), or modelled by Weiner and Conte (1981). But even that addition would ignore competitive aspects that are temporally determined or that are related to vertical rather than horizontal spacing, and would therefore be incomplete.

There is some circumstantial evidence for my hypothesis. The improved survival of seedlings under adult canopies (Friedman and Orshan 1975), the high percentage survival of individuals in clusters of seedlings (this paper, Ebert and McMasters 1981), the finding of only contagious distributions in the Qatari Desert (Ismail and Babikir 1986), and the weak correlation between distance to neighbor or neighbor's size and mortality (Yeaton and Cody 1976, Howe and Wright 1986) all suggest distance between neighbors is of only slight competitive importance in undisturbed desert.

I do not mean to suggest that competition is totally unrelated to horizontal spacing. There have been limited successes at inferring competitive interactions using analyses of spacing (Fowler 1986). The findings that larger (older?) shrubs are regularly spaced, while small ones are random (Phillips and MacMahon 1981, Cody 1986), suggest small effects operating over long periods of time. They could be effects of spatial patterns of moisture use by shrubs and of differences between species in phenologies and root distribution patterns. I suggest these are all small variations on a nearly uniform background of intense competition for water that is largely independent of plant spacing.

ACKNOWLEDGMENTS

I am grateful for the help and suggestions of E. M. Romney, P. D. Greger, R. R. Vance, and J. R. McAuliffe. Work was conducted under contract DE-AMO#-76-SF00012 between the United States Department of Energy and the University of California, with supplemental support from the Nevada Applied Ecology Group, US DOE, Nevada Operations Office.

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AQUATIC INSECTS IN MONTEZUMA WELL, ARIZONA, USA: A TRAVERTINE SPRING MOUND WITH HIGH ALKALINITY AND DISSOLVED CARBON DIOXIDE

Dean W. Blinn[1] and Milton W. Sanderson[1]

ABSTRACT.—An annotated list of aquatic insects from the high carbonate system of Montezuma Well, Arizona, USA, is presented for collections taken during 1976–1986. Fifty-seven taxa in 16 families are reported, including new distribution records for Arizona (*Anacaena signaticollis*, *Laccobius ellipticus*, and *Crenitulus* sp. [nr. *debilis*]) and the USA (*Enochrus sharpi*). Larval stages for Trichoptera, Lepidoptera, Megaloptera, Neuroptera, Chironomidae, and Anisoptera were absent even though the habitat lacks fish, and water temperature, dissolved oxygen, available food, and substrata appear adequate in Montezuma Well. The potential importance of alkalinity in restricting these insect groups is discussed.

Previous collections from the near-constant environment of Montezuma Well, Arizona, have yielded several endemic species of plant and animal taxa (Polhemus 1976, Cole and Watkins 1977, Czarnecki and Blinn 1979, Landye 1981, Davies et al. 1985). Therefore, we believe that a thorough survey of the aquatic insects occupying this high carbonate system was warranted. To date, there have been only a few published reports on the aquatic insects in Montezuma Well. Cole (1965) prepared a list of aquatic insect species in the Well, and Polhemus (1976) described a new heteropteran species (*Ranatra montezuma*) in the Well; Blinn et al. (1982) discussed the nocturnal planktonic behavior of the endemic *Ranatra* species. Recently, Polhemus and Sanderson (1987) reported *Microvelia rasilis* from the Well, which was a new distribution record for the USA.

Montezuma Well is an active, collapsed travertine spring mound in the upper Sonoran Desert grassland of Arizona that has considerably higher concentrations of dissolved CO_2 (>550 mg l^{-1}) and alkalinity (>600 mg l^{-1} $CaCO_3$) than other aquatic habitats in the region. The system encloses an area of 0.76 ha and has a mean depth of 6.7 m (Cole and Barry 1973). The littoral zone supports a dense stand of *Potamogeton illinoensis* Morong; a precipitous drop beyond the submerged vegetation delineates a well-defined pelagic region (0.33 ha, maximum depth 17 m). Warm (24 C) water enters through three or four artesian spring vents at the bottom of the pelagic zone and exits (4,163 l min^{-1}) through a side wall cavern in the travertine deposits (Cole and Barry 1973). The water level remains constant throughout the year, and water temperature never varies more than ± 4.0 C, with an annual mean water temperature of 21.1 C (Boucher et al. 1984). Concentrations of dissolved oxygen are greater than 6.0 mg l^{-1} in the littoral vegetation over a diel period. There are no fish in Montezuma Well, apparently due to high concentrations of dissolved CO_2 (Cole 1983). The high alkalinity of the artesian water maintains a constant pH (6.5, s.d. ± 0.02) and a moderately high specific conductance (925–1,394 μS cm^{-2}, 25 C). Additional physical-chemical information on the Well may be found in Cole and Barry (1973) and Boucher et al. (1984).

METHODS

Seasonal collections were initiated during 1976 and continued through 1986. Samples were taken during both day and night with net tows, grabs, and bottom dredges. The abundance of dominant insect taxa was estimated from harvests of macrophytes taken from circular quadrats (573 cm^2) or vertical 1-m tows with a plankton net (153 μm mesh). Ultraviolet light traps were also employed during night periods to obtain flying adults. Assistance with species identification and/or verification was provided by the following specialists: F. N. Young (Dytiscidae), H. P. Brown (Elmidae), W. U. Brigham (Haliplidae), P. J. Spangler (Hydrophilidae), W. W. Wirth and W. L. Grogan, Jr. (Ceratopogonidae), R. V. Peterson (Diptera), J. Polhemus (Veliidae), D. Bloodgood (Ephemeropta), and D. G. Huggins (Odonata).

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RESULTS AND DISCUSSION

Fifty-seven taxa of aquatic insects in 16 families and 5 orders were collected in Montezuma Well during this study (Table 1). Seven additional taxa have been reported by Cole (1965). We assumed the presence of larval stages indicated that insects reproduced in the Well.

Our collections reported three new records of Coleoptera for the state of Arizona, including *Anacaena signaticollis*, *Crenitulus* sp. (nr. *debilis*), and *Laccobius ellipticus*, and the first records of *Enochrus sharpi* in the United States. In addition, undescribed species of adult *Brachypogon*, *Ceratoculicoides*, *Dasyhelea*, and *Trichomyia* were collected (personal communication, W. L. Grogan and R. V. Peterson) in light traps near the shore of Montezuma Well.

The biting midge family, Ceratopogonidae, had the greatest diversity of species with 30 taxa, while the Hydrophilidae (Coleoptera) were the next most diverse group (7 taxa plus *Hydrophilus* reported by Cole 1965). The soft bottom muds and abundant plant material in Montezuma Well may have provided a variety of suitable substrata for members of the biting midge family. Although not represented by many individual taxa, the Nepidae (*Ranatra montezuma*), Coenagrionidae (*Telebasis salna*), and Mesoveliidae (*Mesovelia mulsanti*) were numerically the most abundant aquatic insects in Montezuma Well. Collections in the top 20 cm of the vegetation yielded 87 nymphs m^{-2} (s.e. ± 21) of *R. montezuma* and 57.4 nymphs m^{-2} (s.e. ± 19.8) of *Mesovelia mulsanti* during the summer, while integrated collections in a 1-m water column in the vegetation yielded 2,119 nymphs m^{-3} (s.e. ± 372) of *Telebasis salna* from June through August.

The absence of major aquatic insect groups in Montezuma Well may be of more ecological interest than the actual occurrence of insect species reported in Table 1. There were no larval representatives of Trichoptera, Lepidoptera, Megaloptera, Neuroptera, Plecoptera, and Anisoptera (Odonata) in our collections from Montezuma Well. In addition to these groups, Chironomidae larvae were also absent, but Cole (1965) reported the occurrence of *Pentaneura* sp. Furthermore, *Callibaetis* (Ephemeroptera) larvae were present in only one collection during July 1986.

The absence of Plecoptera is not surprising because of their strict requirements for clean, cool running waters (Harper and Stewart 1984); however, the absence of Trichoptera, Lepidoptera, Megaloptera, and Anisoptera and the limited collections of Chironomidae and Ephemeroptera are notable since larval stages for these aquatic insects are commonly associated with hydrophytes and/or soft sediments within lakes and ponds (Brigham et al. 1982, Merritt and Cummins 1984). The lack of predaceous fish, the abundance of potential prey (Blinn et al. 1987), the near-constant annual water temperature (21.1 ± 4 C), the adequate dissolved oxygen concentrations (6–14 mg l^{-1}), and the extensive vegetative refuge along the shore of Montezuma Well would appear to provide a suitable habitat for all of these insect groups. Adults of Anisoptera have been observed flying over Montezuma Well and ovipositing, but no nymphs have been collected.

The absence of Trichoptera, Lepidoptera, Megaloptera, Neuroptera, and Anisoptera, as well as the infrequent occurrence of Chironomidae and Ephemeroptera (*Callibaetis*) in Montezuma Well, suggests that high concentrations of dissolved CO_2 (550 mg l^{-1}) and/or alkalinity (600 mg l^{-1} $CaCO_3$) restrict hatching and/or larval development by individuals in these aquatic insect groups, because other physicochemical conditions in the Well appear to be suitable for occupation. This agrees with the findings of Winget and Mangum (1979), who reported a significant negative correlation between alkalinity and number of macroinvertebrate taxa in aquatic ecosystems.

One hypothesis for the restriction of these insect groups is that the high carbonate alkalinity in Montezuma Well may interfere with cutaneous respiratory activities of the immature stages by forming deposits of $CaCO_3$ on the body surface due to a shift in the carbonate equilibrium (Cole 1983). These deposits could greatly reduce the cutaneous surface area

Table 1. Annotated list of aquatic insects from Montezuma Well, Arizona, USA: * indicates new Arizona record; ** indicates new USA record; *** indicates record reported only by G. A. Cole (1965). All identifications for Ceratopogonidae were made from adults, and larval stages were assumed to be present in Montezuma Well.

Coleoptera

Dytiscidae
Celina occidentalis ? (Young)
Cybister ellipticus LeConte
Desmopachria (*Pachriodesma*) *mexicana* Sharp
Neoclypeodytes cinctellus (LeConte)
Thermonectes marmoratus (Hope)

Elmidae
Microcylloepus similis (Horn)

Haliplidae
Peltodytes dispersus Roberts
Peltodytes simplex (LeConte)

Hydraenidae
Ochthebius puncticollis LeConte

Hydrophilidae
**Anacaena signaticollis* (Fall)
Chaetarthria sp.
**Crenitulus* sp. (nr. *debilis* Sharp)
***Enochrus sharpi* Gundersen
****Hydrophilus* sp.
**Laccobius ellipticus* (LeConte)
Tropisternus columbianus Brown

Hydroscaphidae
****Hydroscapha natans* LeConte

Ephemeroptera

Baetidae
Callibaetis sp.

Diptera

Ceratopogonidae
Alluaudomyia needhami Thomsen
Atrichopogon occidentalis Wirth
Atrichopogon transversus Wirth
Atrichopogon sp.
Bessia sandersoni Grogan & Wirth
Brachypogon sp.
Ceratoculicoides sp.
Culicoides brookmani Wirth
Culicoides butleri Wirth & Hubert
Culicoides haematopatus Malloch
Culicoides salihi Khalaf
Culicoides variipennis (Coquillett)
Dasyhelea ancora (Coquillett)
Dasyhelea cincta group (Coquillett)

Table 1 continued.

Dasyhelea fasciigera Kieffer
Dasyhelea grisea group (Coquillett)
Dasyhelea messersmithi Waugh & Wirth
Dasyhelea mutabilis (Coquillett)
Dasyhelea pollinosa Wirth
Dasyhelea pritchardi Wirth
Dasyhelea sp.
Forcipomyia brevipennis (Macquart)
Leptoconops (L.) *torrens* (Townsend)
Palpomyia occidentalis Grogan & Wirth
Parabezzia inermis (Coquillett)
Parabezzia sp.
Phaenobezzia fulvithorax (Malloch)
Stilobezzia antennalis (Coquillett)
Stilobezzia fuscula Wirth
Stilobezzia pruinosa Wirth

Chironomidae
****Pentaneura* sp.

Culicidae
****Anopheles freeborni* Aitken

Psychodidae
Trichomyia sp.

Stratiomyiidae
****Auparyphus* sp.
****Odontomyia* sp.

Heteroptera

Belostomatidae
****Abedus breviceps* Stål
Belostoma bakeri Montandon

Corixidae
Cenocorixa wileyae (Hungerford)

Hydrometridae
Hydrometra aemula Drake

Mesoveliidae
Mesovelia mulsanti White

Naucoridae
Ambrysus woodburyi Usinger

Nepidae
Ranatra montezuma Polhemus
****Ranatra quadridentata* Stål

Veliidae
Microvelia mulsanti White
Microvelia rasilis Drake

Odonata

Coenagrionidae
Enallagma civile (Hagen)
Telebasis salna (Hagen)

available for gas exchange. It has been reported that many aquatic insect larvae, particularly the trichopterans, rely exclusively on the rich tracheal network located just beneath the thin cuticle for gas exchange (Wiggins 1977). Those insect larvae that rely almost exclusively on cutaneous respiration but lack supplemental tracheal gills or the ability to transport air stores may be unable to meet the metabolic demands for oxygen in the high carbonate waters of Montezuma Well. It has also been proposed that the tracheal gills are highly susceptible to damage by environmental extremes since they serve as active uptake sites (Eriksen et al. 1984). The constant low pH (6.5) may also restrict the above described insect groups from Montezuma Well.

ACKNOWLEDGMENTS

This study was supported in part by funds provided to DWB from the Whitehall Foundation, Inc., and an Organized Research Grant from Northern Arizona University. We thank Clay Runck for assistance with the collection and quantification of dominant insect species and the personnel at Montezuma Well, especially Jack Beckman and Jim Coleman, for their excellent cooperation during this study.

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A NEW *HALIPLUS* FROM WARM SPRINGS, NEVADA (COLEOPTERA: HALIPLIDAE)

Samuel A. Wells[1]

ABSTRACT.—*Haliplus eremicus* is described as a new species of the crawling water beetle family Haliplidae. A brief description of the species, illustrations, and diagnosis that compares it with *Haliplus mimeticus* Matheson are provided.

In the early fall of 1984, 11 specimens of *Haliplus eremicus* were collected from a small pond near the Warm Springs recreation area in Nevada. The place is named for the springs that feed a small stream and ponds. *Haliplus eremicus* was collected in a cool pond not far from the stream.

Haliplus eremicus, n. sp.

MALE.—Body broadly oval. Length 3.10–3.60 mm long, 1.70–1.85 times as long as wide.

Head vitelline. Area between eyes 42–46% width of head.

Pronotum vitelline to yellow, 1.75–1.95 times wider than long, 1.55–1.70 times wider at base than at apex, punctate throughout except for a thin, glabrous area slightly basad of center. Prosternum marginate at sides, slightly constricted between procoxae, anterior margin straight.

Elytra cinnamomeus with areas of yellow maculae as follows: along lateral margin with expanded area beginning at basal third and extending distally beyond middle, and mesad to stria 5; macula on disc beginning near elytral base between striae 1 and 3 and extending distally to area one-third the length of elytra from base; macula between striae 2 and 4 joining or adjacent to discal macula and extending distally to area three-fifths length of elytral from base; small macula 0.50 mm long between striae 4 and 5 near base. In one specimen the entire disc is yellow.

Left paramere pale yellow, apex straight and more heavily sclerotized, tuft of long hair one-third length of paramere and one-third distance from apex and base. Aedeagus regularly curved above and below.

FEMALE.—Similar to male.

DIAGNOSIS.—*Haliplus eremicus* (Fig. 1) appears to be most closely related to *H. mimeticus* Matheson (Fig. 2), which was described from one female collected on the Pacific Slope. *Haliplus mimeticus* is unicolorous, whereas *H. eremicus* has light maculae as described above. The anterior margin of the prosternum is sinuate with the median area modestly recurved in *H. mimeticus* (Fig. 4) and straight in *H. eremicus* (Fig. 3). The left paramere in *H. eremicus* (Fig. 6) is more heavily sclerotized at the tip and with the tuft of hair arising more than 0.12 mm from the tip; on *H. mimeticus* the tuft of hair arises 0.10 mm or less from the tip (Fig. 8).

TYPE MATERIAL.—The male holotype, female allotype, and nine paratypes were collected from Warm Springs in Clark County Nevada, 28-IX-1984, by R. W. Baumann, E. Nutall, and myself; one paratype was collected from Tucson, Pima County, Arizona, 25-III-1925, by Bryant, and one was collected from Lakeside, Navajo County, Arizona, 22-VIII-1952, by B. Malkin.

The holotype and allotype are in the U.S. National Museum, four paratypes are in the California Academy of Science, one paratype is at Cornell University, two paratypes are at Brigham Young University, and the remainder are in my collection.

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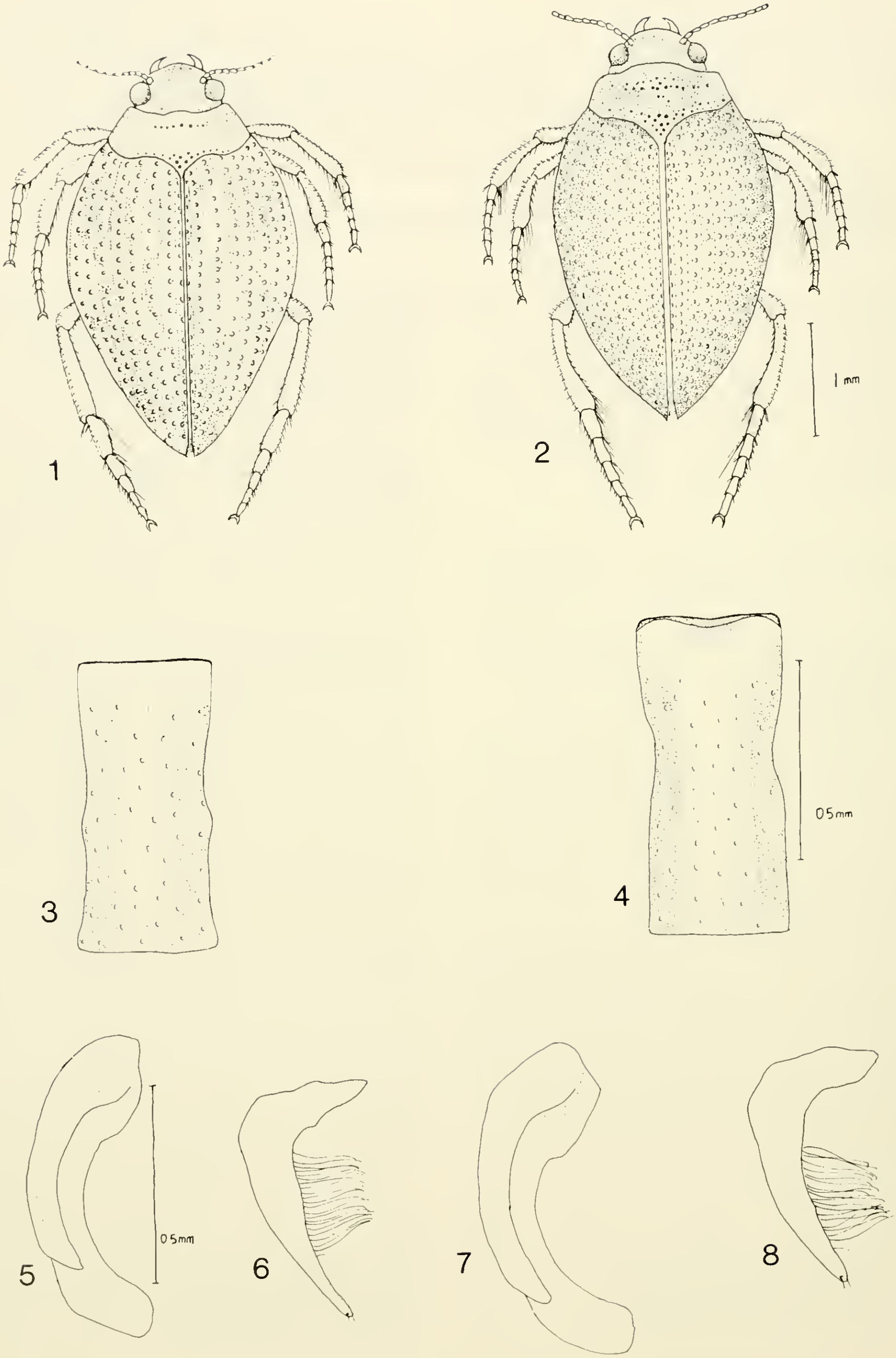

Figs. 1–8. *Haliplus* spp.: 1, *H. eremicus;* 2, *H. mimeticus;* 3, prosternum of *H. eremicus;* 4, prosternum of *H. mimeticus;* 5, aedeagus of *H. eremicus;* 6, left paramere of *H. eremicus;* 7, aedeagus of *H. mimeticus;* 8, left paramere of *H. mimeticus.*

ACKNOWLEDGMENTS

I thank Dr. P. J. Spangler for examining the new species and offering suggestions and Sun Yung Kim for Figures 1–2.

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ON THE GENUS *PARACARINOLIDIA* (CICADELLIDAE: COELIDIINAE: TERULIINI)

M. W. Nielson[1]

ABSTRACT.—Two new species, *Paracarinolidia longiseta* and *P. glabra* from Brazil and French Guiana, respectively, are described and illustrated. A revised key to males of five known species is also presented. The genus is now known to occur in Brazil, Ecuador, Peru, Colombia, and French Guiana.

Paracarinolidia Nielson is a small Neotropical teruliine genus that occurs in a rather broad region from Peru, Ecuador, and Colombia on the west to French Guiana and Brazil on the east. With the addition of two new species described in this paper, there are now five known. Three species occur exclusively in Brazil. One of the new species is from French Guiana, the other from Brazil.

Members of the genus are small and slender, with dark brown to black forewings punctuated with numerous small to large, pale ochraceous markings. The narrow, produced head and carinate lateral margins of the crown are distinctive. These characters together with the long, very slender styles separate the group from its nearest relative, *Carinolidia* Nielson.

Key to Males of *Paracarinolidia*

1. Aedeagus with numerous short to long setae on shaft 2

— Aedeagus without setae or with few very short setae on shaft 4

2(1). Aedeagus with several setae restricted to middle of shaft.................................... 3

— Aedeagus with several setae in apical 1/4 of shaft and with a single, very long, subterminal seta (Figs. 3, 4) .... *longiseta*, n. sp.

3(2). Aedeagus with deep longitudinal cleft medially, setae uniformly short (Nielson 1979, Figs. 87, 88) .... *amabilis* (Linnavuori)

— Aedeagus without such cleft, two setae moderately long, the remainder uniformly short (Nielson 1979, Figs. 79, 80) .... *differta* Nielson

4(1). Aedeagus with few very short setae medially, apex of shaft narrowed, without teeth (Nielson 1979, Figs. 73, 74) .... *guttulata* (Stål)

— Aedeagus without setae, apex of shaft enlarged, with teeth on anterior margin (Figs. 11, 12) ... . *glabra*, n. sp.

Paracarinolidia longiseta, n. sp.

Figs. 1–7

LENGTH.—Male 7.20 mm, female 7.70 mm.

General color dark brown to black with small to large, ivory or pale ochraceous markings on forewings, larger markings at apex of clavus, along costa, and near apex of forewings; small yellowish markings on disk of crown; clypeus and eyes dark brown to black; genae, lorae, and clypellus yellowish.

Head much narrower than pronotum; crown narrow, produced distally beyond anterior margin of eyes, lateral margins distinctly carinate; ocelli near anterior margin of crown; eyes large, nearly globular; pronotum short, median length less than median length of crown; scutellum moderately large, median length greater than median length of pronotum; forewings elongate, venation typical; clypeus long and narrow, with prominent median longitudinal carina; clypellus narrow, lateral margins nearly parallel.

MALE.—Pygofer with long, narrow, caudodorsal lobe and very short, caudoventral lobe (Fig. 1); aedeagus asymmetrical, tubelike in ventral view, constricted subapically and curved dorsally at apex, with several short setae subapically and one long, subterminal seta extending basally in lateral view (Figs. 3, 4), gonopore near middle of shaft on ventral surface; style long and slender in distal 2/3, enlarged at basal 1/3, tapered distally (Figs. 5, 6); plate long and moderately broad medially with few short distal setae (Fig. 2).

FEMALE.—Seventh sternum with caudal margin broadly bilobed (Fig. 7).

HOLOTYPE (male).—BRAZIL: Rondonia, Vilhena, 3.VIII.1983, Norman Penny (INPA).

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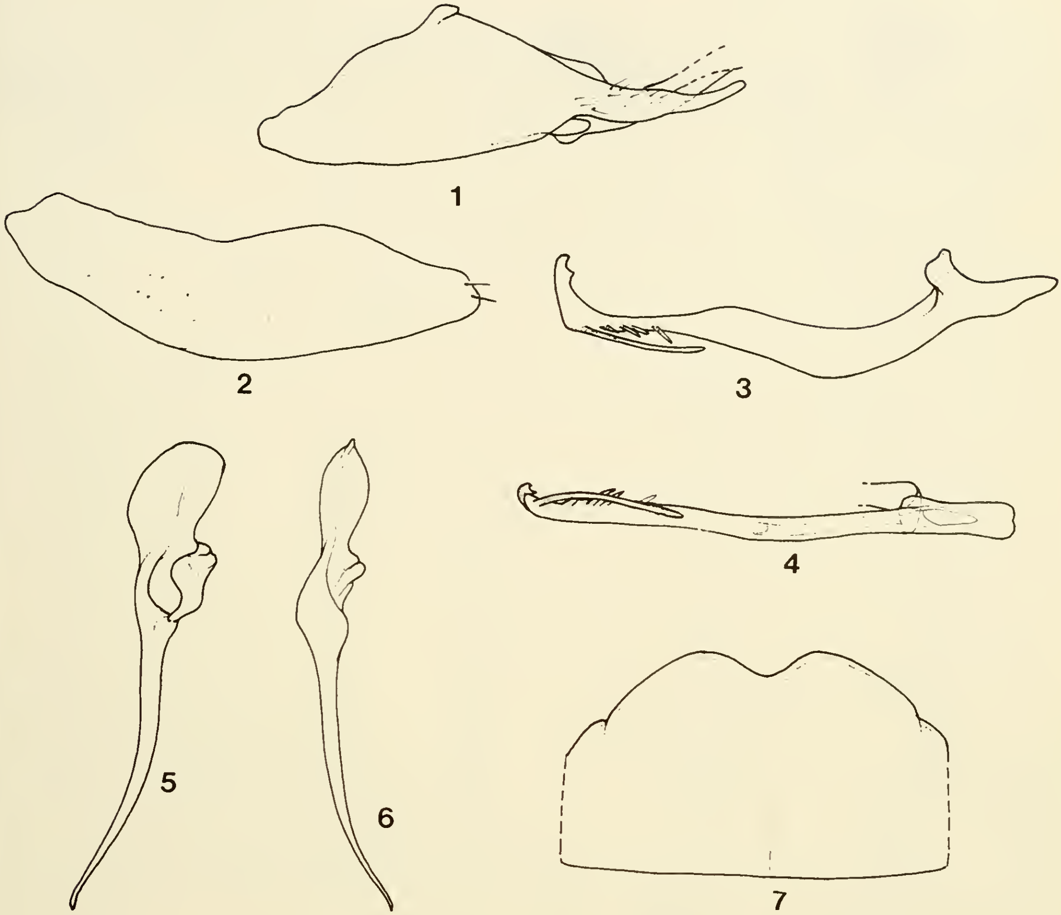


Figs. 1–7. *Paracarinolidia longiseta*, n. sp.: 1, male pygofer, lateral view; 2, plate, ventral view; 3, aedeagus, lateral view; 4, aedeagus, ventral view; 5, left style, dorsal view; 6, left style, lateral view; 7, female seventh sternum, ventral view.

Allotype (female), same data as holotype except 29.VII.1983 (INPA).

REMARKS.—This species is nearest to *differta* Nielson and can be distinguished by a row of short setae on the apical 1/4 of the aedeagal shaft with a long, subterminal seta.

Paracarinolidia glabra, n. sp.

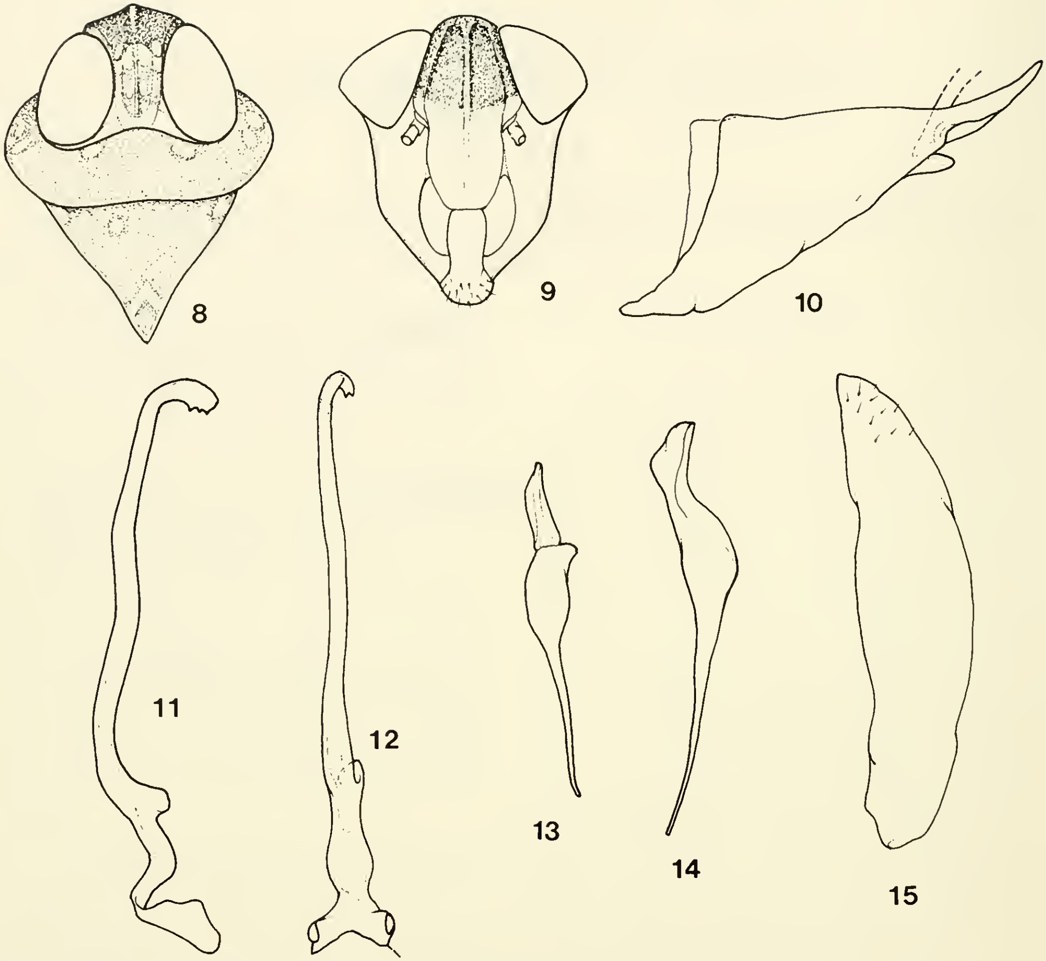
Figs. 8–15

LENGTH.—Male 6.90 mm.

General color as in *longiseta;* costal spots on forewing smaller, spot in 5th apical cell much reduced; markings on crown and face similar to *longiseta*. Similar in size and male genitalia to *guttulata*.

Head much narrower than pronotum (Fig. 8); crown very narrow, produced distally beyond anterior margin of eyes, width much narrower than width of eyes, lateral margins distinctly carinate; eyes very large, nearly globular; pronotum short, median length shorter than median length of crown; scutellum moderately large, median length greater than median length of pronotum; forewing elongate, venation typical (right forewing missing in type); clypeus long and narrow, with prominent median longitudinal carina; clypellus narrow, lateral margins expanded distally (Fig. 9).

MALE.—Pygofer as in *longiseta* (Fig. 10); aedeagus asymmetrical, tubular throughout



Figs. 8–15. *Paracarinolidia glabra*, n. sp.: 8, head, pronotum, and scutellum, dorsal view; 9, same, ventral view; 10, male pygofer, lateral view; 11, aedeagus, lateral view; 12, aedeagus, ventral view; 13, right style, ventral view; 14, right style, lateral view; 15, plate, ventral view.

shaft, slightly sinuate, without setae on shaft, apex curved dorsally and toothed on anterior margin (Figs. 11, 12), gonopore near middle of shaft; style very narrow in distal half (Figs. 13, 14); plate long and moderately broad, with several setae distally (Fig. 15).

FEMALE.—Unknown.

HOLOTYPE (male).—FRENCH GUIANA (Cayenne): Oyac-Conti-Cacao-Bief,—.IX–X.1914, R. Benoist (MNHN).

REMARKS.—*Paracarinolidia glabra* is similar in male genital characters to *P. guttulata* but can be separated by the lack of aedeagal setae and by the shorter style. The internal male genital structures (aedeagus, connective, and styles) of the holotype specimen were apparently lost after they were illustrated. The abdomen, pygofer, and plates remain in the attached microvial.

ACKNOWLEDGMENTS

I thank Dr. Norman Penny, formerly of Instituto Nacional de Pesquisas da Amazonia (INPA), now with California Academy of Science, San Francisco, and Dr. Michel Boulard, Museum National d'Histoire Naturelle, Paris (MNHN), for the loan of specimens described in this paper. I appreciate the fine illustrations prepared by Mrs. Jeanette Price; and for reviewing the manuscript, I express my gratitude to Dr. Paul Freytag, University of Kentucky, Lexington.

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TWO NEW GENERA AND TWO NEW SPECIES OF TERULIINE LEAFHOPPERS (HOMOPTERA: CICADELLIDAE: COELIDIINAE)

M. W. Nielson[1]

ABSTRACT.—Two new genera and two new species of leafhoppers in the tribe Teruliini are described and illustrated. New genera include: *Perspinolidia*, type-species *Perspinolidia peruviensis*, n. sp., and *Brevicapitorus*, type-species *Brevicapitorus elongatus*, n. sp. Both genera are monobasic and occur in the Neotropical region.

Two genera and their attendant species described in this paper represent a continuum of new taxa of a leafhopper group whose presence is rare in the Neotropical region. Only a few specimens are usually collected at any given time, but they add generic diversity and taxonomic composition to the tribe Teruliini (Nielson 1979, 1983a, 1983b). There are now 47 genera assigned to the tribe, 23 of which are monobasic.

The genus *Perspinolidia* represents an anomaly in characterization of the tribe. The median longitudinal clypeal carina, which separates the tribes Teruliini and Coelidiini, is incomplete in *Perspinolidia* and does not reach the anterior margin from its origin at the transclypeal suture. This deficiency may denote variability in the length of the character or an evolutionary state of development in which the carina is being added to or deleted from the clypeus. In either case, the genus is more closely related to members of Teruliini than to members of any other tribe in the subfamily Coelidiinae.

Perspinolidia, n. gen.

TYPE-SPECIES.—*Perspinolidia peruviensis*, n. sp.

Medium-sized, robust species. Similar in general habitus to *Articoelidia* Nielson but with distinctive male genitalia. General color dark brown with suffused light brown on clavus extending to apex of forewing.

Head narrower than pronotum; crown broad, width greater than width of eyes; eyes large, semiglobular; pronotum and scutellum large; forewings with 5 apical cells, 3 anteapical cells present, outer one closed; clypeus long and broad, with incomplete median longitudinal carina, originating at the transclypeal suture but not reaching anterior margin; hind femoral setal arrangement 2+2+1.

Male genitalia partly asymmetrical; pygofer with small caudodorsal lobe; aedeagus asymmetrical, long, somewhat tubular with tuft of setae distad of middle near large gonopore on lateral margin; connective Y-shaped with short stem; style large, very broad in lateral view; plate long, broad subapically, setaceous.

The genus keys to *Articoelidia* in couplet 21 in Nielson (1979), but it can be distinguished by the lack of prominent spines on the pygofer and segment 10, the presence of the broad style, and the subdistal tuft of setae on the aedeagus.

Perspinolidia peruviensis, n. sp.

Figs. 1–8

LENGTH.—Male 8.70 mm.

General color dark brown. Crown light tannish; pronotum black except for tan anteriolateral margins; scutellum black; forewings dark brown to black except for light brown from base of clavus to apex of wing, costal area light brown; face tan. Similar in general habitus to species of *Articoelidia*, but with distinctive male genitalia.

Head narrower than pronotum (Fig. 1); crown produced and rounded anteriorly, broad, width much greater than width of eyes; eyes large, semiglobular; pronotum moderately long, median length about as long as median length of crown; scutellum large, median length greater than median length of pronotum; forewing and venation typical;

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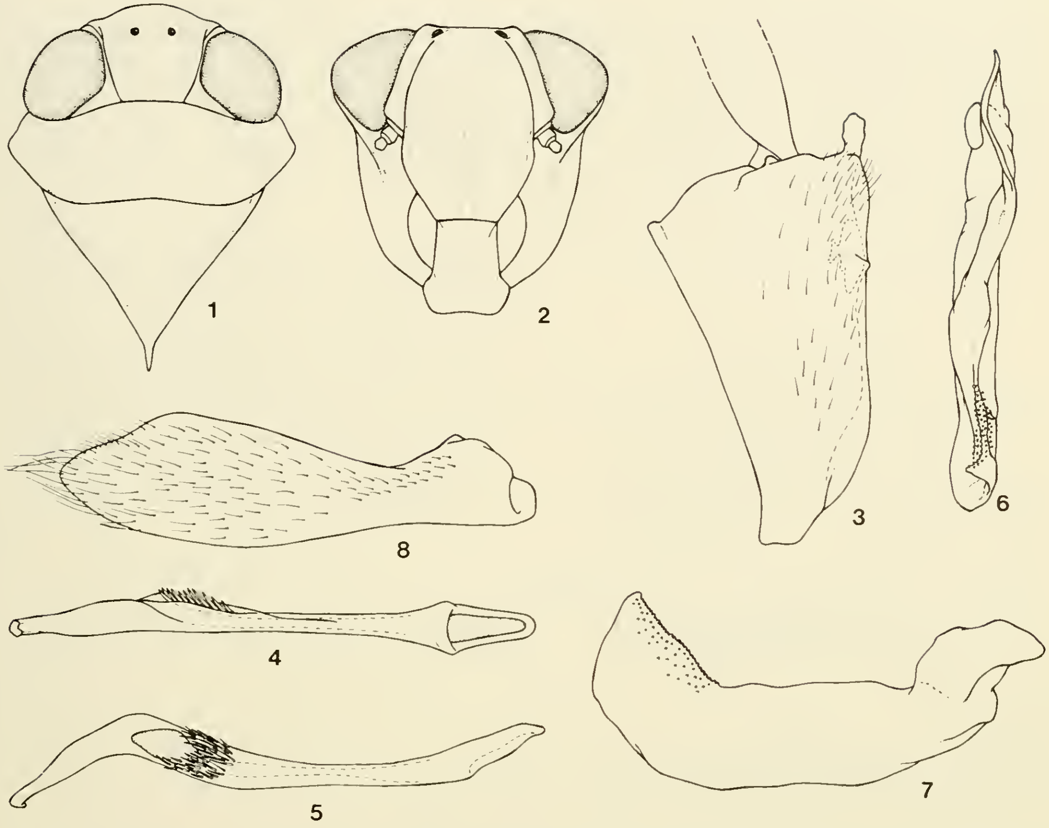


Figs. 1–8. *Perspinolidia peruviensis*, n. sp.: 1, head, pronotum, and scutellum, dorsal view; 2, face, ventral view; 3, male pygofer, lateral view; 4, aedeagus, dorsal view; 5, aedeagus, lateral view; 6, style, dorsal view; 7, style, lateral view; 8, plate, ventral view.

clypeus long and broad, somewhat tumid, with incomplete median longitudinal carina arising at base of transclypeal suture and extending anteriorly to about 2/3 length of clypeus (Fig. 2).

MALE.—Pygofer with small caudodorsal lobe directed dorsally (Fig. 3); aedeagus asymmetrical, long, somewhat tubular, sinuate in lateral view and tapered toward apex, with tuft of dense, stout setae on lateral margin just basad of gonopore (Figs. 4, 5), gonopore large, subdistal on lateral margin; style large, compressed laterally and very broad in lateral view, dentate apically on dorsal margin (Figs. 6, 7); plate moderately long, lateral margins expanded before apex (Fig. 8).

FEMALE.—Unknown.

HOLOTYPE (male).—PERU: Río Santiago, 30.IX.1924. H. Bassler, F–6137, Acc. 33591 (AMNH).

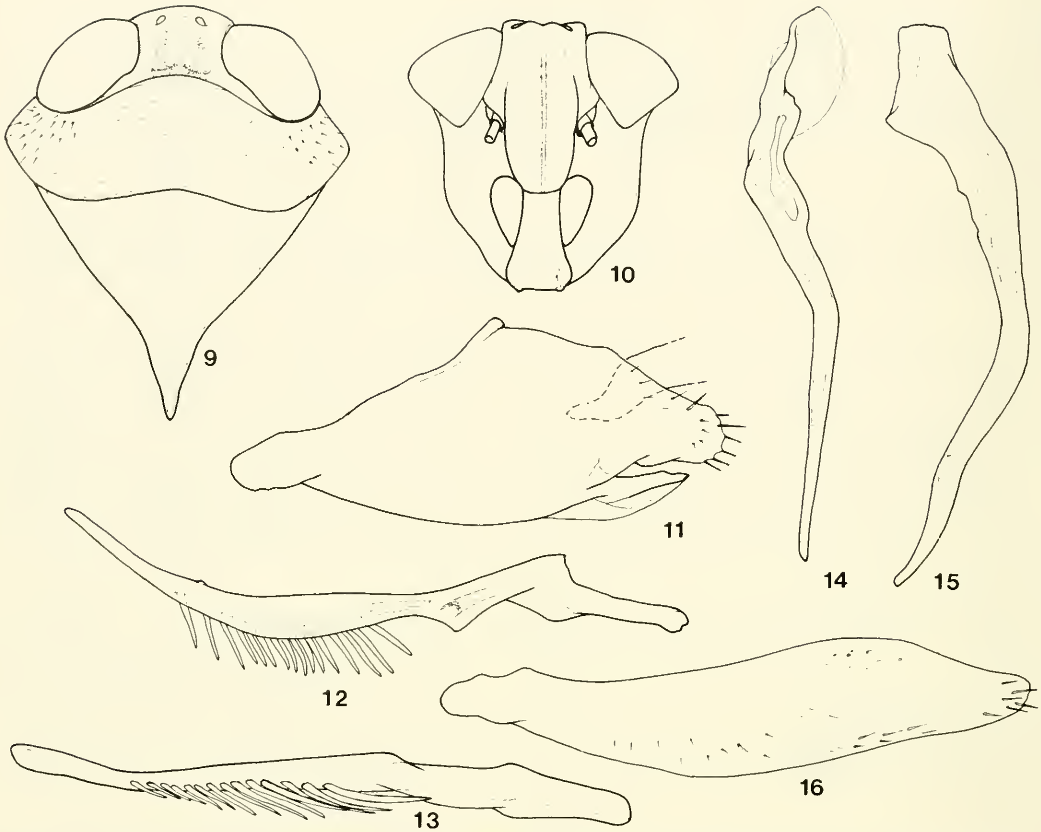
REMARKS.—*Perspinolidia peruviensis* is the only known species in the genus, and it can be distinguished from members of *Articoelidia* by the incomplete median clypeal carina, by the lack of spines on the pygofer and segment 10, and by the presence of a subdistal tuft of setae on the aedeagus.

Brevicapitorus, n. gen.

TYPE-SPECIES.—*Brevicapitorus elongatus*, n. sp.

Medium-sized, robust species. Similar in general habitus to large species of *Docalidia* Nielson, but with distinctive male genitalia. General color black.

Head distinctly narrower than pronotum; crown short, broad, about as wide as eyes; eyes large, semiglobular; pronotum and scutellum large; forewings with 5 apical cells, 3 anteapical cells present, outer one closed;



Figs. 9–16. *Brevicapitorus elongatus*, n. sp.: 9, head, pronotum, and scutellum, dorsal view; 10, face, ventral view; 11, male pygofer, lateral view; 12, aedeagus, lateral view; 13, aedeagus, ventral view; 14, style, dorsal view; 15, style, lateral view; 16, plate, ventral view.

clypeus long and narrow, with complete median longitudinal carina; hind femoral setal arrangement 2+2+1.

Male genitalia partly asymmetrical; pygofer with large caudoventral lobe; aedeagus asymmetrical, long, somewhat tubular with single row of stout setae along middle, gonopore subbasal; connective Y-shaped with short stem; style very long; plate long, narrow.

The genus keys near *Terulia* Stål in couplet 5 of Nielson (1979) and can be separated by a row of stout setae along the middle of the aedeagus and by the very short, rounded head.

Brevicapitorus elongatus, n. sp.

Figs. 9–16

LENGTH.—Male 9.70–9.90 mm.

General color black. Crown and eyes light tannish brown, disk blackish in basal half; pronotum and scutellum black; forewings dark brown to black, veins black; face black. Similar in general habitus to species of *Docalidia* but with distinctive male genitalia.

Head much narrower than pronotum (Fig. 9); crown short, rounded anteriorly, disk broad, width nearly equal to width of eyes; eyes large, semiglobular; pronotum large, median length much greater than median length of crown; scutellum large, median length greater than median length of pronotum; forewing broad, apex acutely angled, venation typical; clypeus long and narrow, with prominent median longitudinal carina (Fig. 10); clypellus long, lateral margins expanded distally.

MALE.—Pygofer with broad caudoventral lobe (Fig. 11); aedeagus asymmetrical, long, somewhat tubular in dorsal view, slightly curved in lateral view and expanded between apex and gonopore, with single row of stout setae along middle of shaft, setae directed more or less laterally (Figs. 12, 13), gonopore subbasal on lateral surface; style very long, nearly as long as aedeagus, curved in dorsal and lateral views, tapered distally (Figs. 14, 15); plate long and narrow, sparsely setose (Fig. 16).

FEMALE.—Unknown.

HOLOTYPE (male).—BRAZIL: Sinop, Matto Grosso, —.X.1975, M. Alvarenga (UFP). Paratype, one male? (abdomen missing), same data as holotype (author's collection).

REMARKS.—This species is the only known representative of the genus, and it can be separated from members of the genus *Docalidia* by the single row of stout spines on the middle of the aedeagal shaft.

ACKNOWLEDGMENTS

The leafhopper specimens were kindly furnished by Dr. Jerome Rozen, American Museum of Natural History, New York (AMNH), and Dr. Keti Maria Rocha Zanol, Universidade Federal do Paraná, Curitiba, Paraná (UFP). The excellent illustrations were prepared by Jean Stanger, and the manuscript was reviewed by Ray Gill, California Department of Food and Agriculture, Sacramento. To all of these colleagues I extend my sincere gratitude for their help.

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A NEW SPECIES OF *ASCLEPIAS* (ASCLEPIADACEAE) FROM NORTHWESTERN NEW MEXICO

Kenneth D. Heil[1], J. Mark Porter[2], and Stanley L. Welsh[3]

ABSTRACT.—*Asclepias sanjuanensis* Heil, Porter, & Welsh, a new species from the pinyon-juniper woodlands of the San Juan River Valley, San Juan County, New Mexico, is described and illustrated. The species appears to be local and rare. Similar to *A. ruthiae* Maguire, it is distinguished by the greater number of flowers per inflorescence, the larger number of stems, and the pubescence characters.

A new species of *Asclepias* was discovered among specimens taken recently from the San Juan Valley of northwestern New Mexico. The rare new entity apparently falls into the subgenus Asclepiodella (Small) Woodson according to Woodson (1954). The subgenus is represented by *A. ruthiae* Maguire in Maguire & Woodson, *A. eastwoodiana* Barneby, *A. cutleri* Woodson, *A. cordifolia* (Benth.) Jepson, *A. brachystephana* Torr., and *A. uncialis* Greene, all occurring in western North America. Additional species, *A. cinerea* Walt. and *A. feayi* Chapm. ex Gray, occur in the eastern United States. The species described herein was discovered by Barbara Jenkins, Londa Smith, and Marc Werthington while performing a floristic study of the Fred Edwards Wilderness Walk at San Juan College, Farmington, New Mexico, during the spring of 1988. Following the initial discoveries, a survey of surrounding areas was conducted to ascertain the distribution of the taxon. The plant is described as follows.

Asclepias sanjuanensis **Heil, Porter, & Welsh,** sp. nov.

Asclepiate ruthia Maguire affinis sed in floribus et caulibus plus numerosis et pubescentis differt.

Herbaceous perennial; stems prostrate to ascending, 4–8.3 cm long, glabrous below, becoming minutely tomentulose above, branched below ground, with 2–7 stems from a woody taproot; lowermost leaves scalelike; leaves (1) 2–4 cm long, 0.4–2.5 cm broad, oblong-lanceolate, narrowly acute, approximate to opposite, petiolate, the petiole 0.2–0.5 cm long, white tomentulose on leaf margins and midrib of abaxial leaf surface only; inflorescence terminal, rarely axillary, sessile, sparsely pilosulose, umbelliform cyme, with 4–15 flowers; pedicels 1.2–2.8 cm long; flowers small; calyx lobes lanceolate, 1.8–3.2 mm long, reflexed; corolla reflexed-rotate, pale violet, the lobes 3.5–6 mm long; column 0.4–0.7 mm high, ca 1.3–3 mm thick, reddish green; hoods 1.5–2.5 mm long, saccate, truncate, reddish violet with cream to yellowish margins, glabrous, the marginal auricles more or less erect, lanceolate; horn ca 2.3 mm long, included to barely exserted from the hood, attached near the middle and erect from it; anther head 1.9–3 mm high, ca 1.3–2 mm in diameter, the wings narrow; pollinarum ca 0.23 mm long, the corpusculum ca 0.08 mm long, ca 0.04 mm wide, the translator arm ca 0.07 mm long, the pollinia 0.15 mm long; follicle 3.5–6.5 mm long, 1.1–1.6 mm wide, puberulent, smooth, erect on a reflexed pedicel; seeds ca 1 mm long.

TYPE.—USA: New Mexico, San Juan County, Farmington, along the Fred Edwards Wilderness Walk on the campus of San Juan College; T30N, R13W, S35, NW 1/4, 22 May 1988, K. D. Heil 4338 (Holotype BRY; Isotypes ARIZ, MO, NY, NMC, SJNM).

Asclepias sanjuanensis occurs on sandy or sandy loam soils, usually in disturbed sites, i.e., erosion channels, trails (human or animal), and two-track roadways. The populations are known from 1,524 to 1,676 m on

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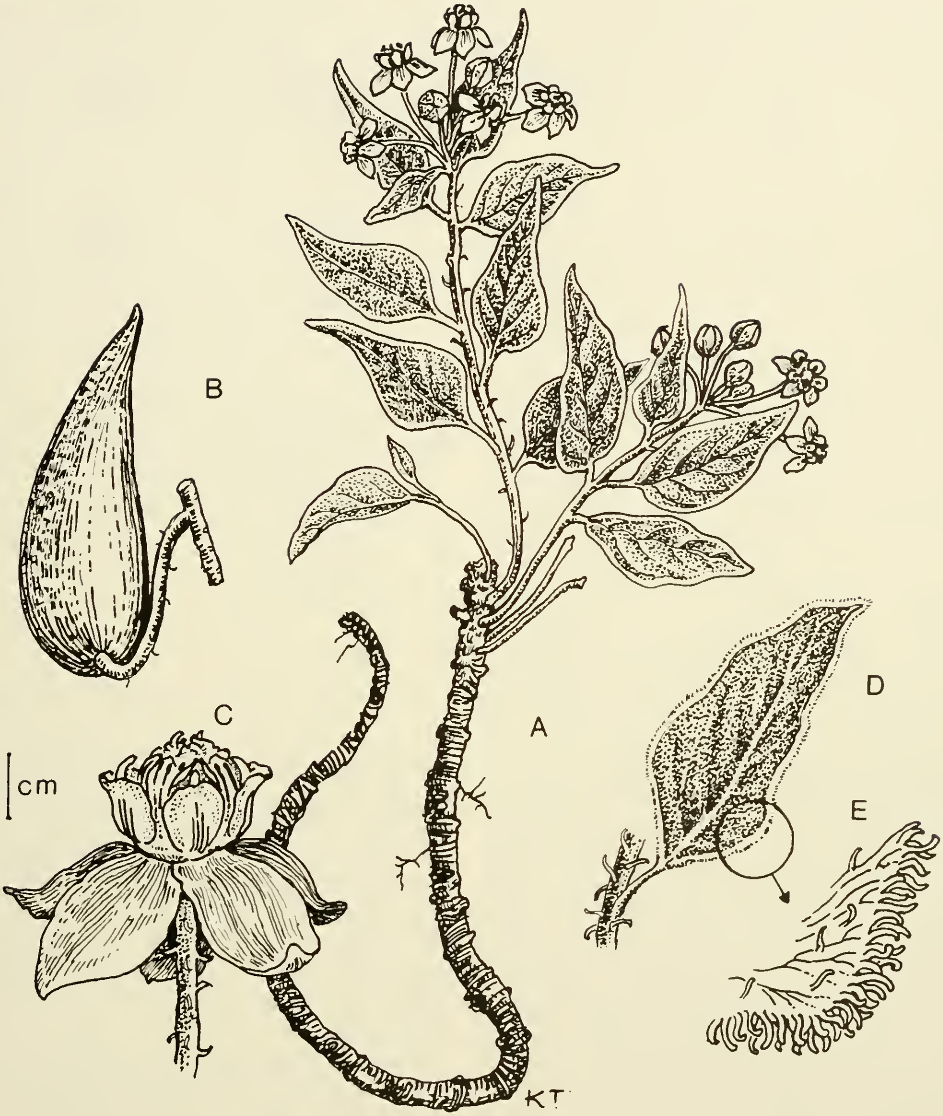

Fig. 1. *Asclepias sanjuanensis:* A, habit; B, follicle; C, flower; D, leaf; E, enlargement of cilliate leaf margin.

slopes and floodplains of the San Juan River Valley. They occur in pinyon-juniper woodlands (with *Pinus edulis, Juniperus osteosperma, Quercus gambelii, Purshia tridentata, Mirabilis multiflora, Eriogonum microthecum,* and *Penstemon ophianthus.* Subsequent to the initial discovery, two additional collections were made at Farmington and near Bloomington, New Mexico. Only solitary plants were found at both of those locations. Preliminary field investigations indicate that the taxon is a local endemic in a region approximately 33 km in length along the San Juan River. The plants flowered first between early and late April in 1988 and continued to flower into May. Fruit matured by mid-June.

The sessile or essentially sessile, erect, open hoods, which possess a deeply saccate basal attachment, are characters that associate *A. sanjuanensis* with members of subgenus Asclepiodella. The species is a near congener of both *A. ruthiae* and *A. eastwoodiana,* with which it can be easily confused. However, it is

TABLE 1. Morphological and ecological comparison of *Asclepias sanjuanensis*, *A. ruthiae*, *A. eastwoodiana*, and *A. cutleri*.

Character	*sanjuanensis*	*ruthiae*	*eastwoodiana*	*cutleri*
Number of flowers	4–15 (mean = 10)	2–6	3–5(14)	3–5(7)
Number of branches	2–7	1(2)	1(3)	1(2)
Herbage pubescence	sparsely puberulent	densely puberulent	sparsely puberulent	appressed puberulent
Hood pubescence	glabrous	puberulent or glabrous	glabrous	glabrous
Auricles of hood	erect	obscure, not erect	erect	erect
Leaf shape	lanceolate to broadly lanceolate	broadly ovate to broadly lanceolate	lanceolate to broadly ovate	filiform
Leaf pubescence	margins and veins	dense on entire surface	margins and veins	entire surface
Habit	prostrate to ascending	prostrate	prostrate to ascending	erect–ascending
Habitat	disturbed	undisturbed to disturbed	disturbed	disturbed
Locale	NW New Mexico	SE Utah, N Arizona	Central Nevada	SE Utah, N Arizona

allopatric with both of those taxa. The close relationship between *A. ruthiae* and *A. eastwoodiana* is not disputed (Cronquist et al. 1984); in fact, these taxa were at one time considered conspecific (Woodson 1954). *Asclepias sanjuanensis* fits well into this species group based on morphological and ecological characteristics (Table 1). It differs from *A. ruthiae* by the greater number of flowers per inflorescence, the larger number of branches from the summit of the root crown, the leaf pubescence characters, the leaf shape, and the erect auricles. From *A. eastwoodiana* it differs in flower number (but not as greatly as from *A. ruthiae*) and in the number of branches from the root crown.

It appears that *A. sanjuanensis* is most like the remote *A. eastwoodiana*, which occurs in central Nevada (Barneby 1945, Cronquist et al. 1984). Between these two species is the much more widespread *A. ruthiae*, which occurs in southeastern Utah and north central Arizona (Welsh et al. 1987, Cronquist et al. 1984). It seems probable that both *A. sanjuanensis* and *A. eastwoodiana* diverged from an ancestral series now called *A. ruthiae*. Possibly the similarities between the two geographical isolates are the result of parallel evolution.

Asclepias cutleri Woodson is quite distinct morphologically from the aforementioned western members of this complex (e.g., appressed pubescence and filiform leaves). *Asclepias brachystephana*, located from Trans-Pecos Texas to southern Arizona and south to central Mexico, differs in its linear lanceolate leaves, its sparse, more or less appressed pubescence of the leaves, and its ascending to erect habit.

Asclepias sanjuanensis is, however, strikingly similar to these and other members of the subgenus in its ecological adaptations. *Asclepias cutleri* is adapted to unstabilized sand and is conspicuously absent from undisturbed localities. Likewise, *A. eastwoodiana*, *A. cordifolia*, and *A. brachystephana* are adapted to sites that undergo continuous erosion or prolonged disturbance, usually sandy or alkaline clay sites. We reject the proposition that these are pioneer species of succession but, rather, believe they are species highly adapted to sites that undergo continual disturbance, e.g., erosion channels, wash slopes, and dunes. *Asclepias eastwoodiana* is associated with highly erodable alkaline clay hills. *Asclepias cordifolia* grows on gravel hills or talus slopes. *Asclepias ruthiae*, while found occasionally on undisturbed habitats, grows often in areas of shifting sands and in gullies and other erosion channels (Cronquist et al. 1984).

Until a detailed study of *Asclepias* is undertaken, the relationships of this complex to other subgenera will remain unclear. Barneby (1945) suggested that *A. eastwoodiana* is closely allied to *A. involucrata* Engelm. ex Torr., considered by Woodson (1954) to be within subgenus Asclepias, series Macrotides. We do not consider *A. sanjuanensis* to be closely allied to *A. involucrata.*

ACKNOWLEDGMENTS

Much credit is due the systematic botany students Barbara Jenkins, Londa Smith, and Marc Werthington for the discovery of this plant. We thank Fred Edwards for searching for populations in the San Juan College area and acknowledge Kaye Hugie Thorne for the illustrations.

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EFFECT OF TIMING OF GRAZING ON SOIL-SURFACE CRYPTOGAMIC COMMUNITIES IN A GREAT BASIN LOW-SHRUB DESERT: A PRELIMINARY REPORT

James R. Marble[1] and Kimball T. Harper[1]

ABSTRACT.—Cover and species richness of vascular and cryptogamic components of the plant community were inventoried in experimental grazing paddocks at the USDA/FS Desert Range Experimental Station, Millard County, Utah. The grazing treatments considered have been applied continuously for over 50 years. The effects of heavy (ca 17 sheep days/acre) grazing treatment applied in two different seasons (early winter versus a split between early and late winter) differed significantly between seasons. Cryptogamic cover and cryptogamic species richness both showed larger decreases under early-late as opposed to early winter only grazing. Vascular plant cover (relative to controls) was also reduced by early-late winter grazing, but not to a significant degree. Late season grazing, likewise, had no significant effect on number of vascular species per transect.

The importance of cryptogamic plants (algae, mosses, and lichens) as soil stabilizers on Great Basin rangelands has only recently been appreciated by range managers. Management strategies that retain the positive effects of these nonseed plants, without eliminating grazing animals from the land, have not yet been established. It is our purpose here to report the effects of different seasons of sheep grazing on cryptogamic plant covers at the Desert Range Experimental Station in west central Utah.

Communities of nonvascular cryptogamic plants grow on or just below the soil surface. The organisms that coexist in such communities include species of fungi, algae, lichens, and mosses. When well developed, the crusts play an important role in soil stabilization in deserts (Fletcher and Martin 1948, Kleiner and Harper 1972, 1977, Loope and Gifford 1972, Anderson et al., Recovery, 1982, Anderson et al., Factors, 1982). The effects of cryptogamic crusts on infiltration and sediment release were studied by Loope and Gifford (1972). More recent studies have demonstrated the importance of cryptogamic crust in reducing soil erosion and increasing water infiltration. Lusby et al. (1963, 1971) and Lusby (1979) studied the effect of grazing and sediment yield on western Colorado watersheds. Although Lusby and collaborators did not record cryptogamic cover directly, their results are congruent with the hypothesis that biological crusts are important in the soil stabilization process at that site. They found that altering the season of grazing from winter long (15 Oct.–15 May) to early winter only (15 Oct.–15 Feb.) without a change in grazing intensity reduced water runoff by 23% and sediment release by 31%. Lusby et al. (1963, 1971) and Lusby (1979) could not demonstrate a significant change in vascular plant cover associated with the large changes in runoff and sediment release. Harper and St. Clair (1985) found that physical disruption of cryptogamic crusts (as might be caused by trampling by herds of hooved animals) increased the average loss of water as runoff by 51% and increased soil loss by 686%. Complete removal of the crust resulted in the loss of 92% more water than was lost from control plots and 1,441% more soil loss.

The analysis of species composition of cryptogamic covers has been facilitated by the work of Anderson and Rushforth (1976). They provided photos and/or line drawings of the major algal, moss, and lichen components of cryptogamic crust communities in the Intermountain West. The role of cryptogamic crusts in nitrogen fixation has been studied by Rychert and Skujins (1974). The impact of 40 years of uncontrolled grazing on a soil cryptogam community in Navajo National Monument, Arizona, was studied by Brotherson et al. (1983). They found considerable damage to the cryptogamic community and less stable soil conditions where grazing had been permitted. They recommended that future range research should include analysis of factors that favor persistence of cryptogamic crusts and the impact of established grazing systems on those microplant assemblages.

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SITE DESCRIPTION

The study area is located at the Desert Range Experimental Station in Millard County, southwestern Utah. Since the Forest Service, U.S. Department of Agriculture, established the Desert Experimental Range (DER) in 1934, the vegetational consequences of three intensities of grazing (light, moderate, and heavy) have been tested in all possible combinations with three different grazing seasons (early, mid-, and late winter). Each combination of intensity and time was replicated twice. Each treatment was applied to a separate 240-acre pasture. Each pasture contains two exclosures that initially had plant cover comparable to that on the remainder of the pasture. The 1-acre (0.40-ha) exclosures have been ungrazed throughout the period of study.

METHODS

Within each of two grazed pastures (one heavily grazed in early winter and the other grazed at the same intensity but with half of the use applied in early winter and the remainder in late winter), four sets of paired transects were read. The heavy grazing treatment consisted of 17 sheep days of use per acre. Each grazed transect was paired with a transect approximately 16 m away and within a control exclosure. Each transect consisted of cover estimates at 10 subsample points. Cover readings were made using a nested frequency quadrat with eight points per subsample. The 0.25-m^2 frequency quadrat was subdivided into three smaller quadrats nested within; the sizes of the four nested quadrats were 0.25, 0.125, 0.0625, and 0.0025 m^2. Cover percentages were based on the number of points intercepting each cover type. Percent cover for any cover type was computed by dividing the number of points intercepting that type by all points read along the transect (always 80) and multiplying by 100.

The effect of each grazing treatment was analyzed in terms of cover and species richness (species per transect) for the following cover parameters: absolute cryptogamic, absolute vascular, and percent of total contributed by cryptogams (cryptogamic/total). The mean value for each class along each transect was used as a single datum to avoid pseudoreplication. Data were compared using the paired t-test (Zar 1974).

RESULTS

The early-late winter grazing treatment showed significant differences between control and treatment plots in respect to both cryptogamic cover and number of cryptogamic species as a percentage of total species (Tables 1, 2). The average number of cryptogamic species per transect and the average percent of total species contributed by cryptogamic species were significantly reduced relative to controls under early-late winter grazing (Table 2). Neither vascular plant cover nor the number of vascular species differed significantly between control and treatment plots. Early winter grazing treatment showed no significant differences for any variable.

DISCUSSION AND CONCLUSIONS

A significant reduction in cryptogamic cover is associated with late winter grazing as indicated by readings of absolute cryptogamic cover and cryptogamic cover as a percent of total living cover. Late winter grazing, however, did not significantly reduce vascular cover. The early winter grazing treatment, in contrast, showed no significant difference in any cover type between treatment and control plots.

Species richness comparisons show the same pattern of response to grazing season as cover comparisons. Early-late winter grazing significantly reduced both absolute cryptogamic species richness and cryptogamic species as a percentage of total species. Early winter grazing, on the other hand, did not significantly reduce either absolute number of cryptogamic species or cryptogamic species as a percentage of all species. The number of vascular species was not significantly reduced under either grazing treatment.

Table 1. Cover values for cryptogamic and vascular plant species on grazed and ungrazed transects. Grazed transects are used at the same intensity (heavy) but in different combinations of seasons. Asterisked t-values denote significant differences between treatments and controls.

	Percent cover		Cryptogamic species as % of total
Treatment	Cryptogamic	Vascular	
Early winter			
Grazed transect			
1	0.0	7.5	0.0
2	0.0	18.8	0.0
3	1.3	27.5	4.5
4	0.0	27.5	0.0
Averages	0.3	20.3	1.1
Control transect			
1	1.3	21.1	5.8
2	2.5	1.3	65.8
3	0.0	23.8	0.0
4	1.3	16.3	7.4
Averages	1.3	15.6	19.8
(t-values)	1.192	0.694	1.457
Early-late winter			
Grazed transect			
1	0.0	15.0	0.0
2	0.0	11.3	0.0
3	0.0	15.0	0.0
4	0.0	20.0	0.0
Averages	0.0	15.3	0.0
Control transect			
1	2.5	26.3	8.7
2	3.8	15.0	20.2
3	7.5	21.3	26.0
4	5.0	20.0	20.0
Averages	4.7	20.6	18.7
t-values	4.392*	2.251	5.153*
	$t_{0.05,(2),3} = 3.182$		

Table 2. Species richness values for cryptogamic and vascular plant species on grazed and ungrazed transects. Grazed transects are used at the same intensity (heavy) but in different combinations of seasons. Asterisked t-values denote significant differences between treatments and controls.

	No. of species/transect		Cryptogamic species as % of total
Treatment	Cryptogamic	Vascular	
Early winter			
Grazed transect			
1	1	13	7.1
2	1	12	7.7
3	4	10	28.6
4	2	8	20.0
Averages	3.8	10.8	15.9
Control transect			
1	4	10	28.6
2	4	14	22.2
3	4	12	25.0
4	4	11	26.7
Averages	4	11.8	25.6
t-values	2.333	0.739	1.460
Early-late winter			
Grazed transect			
1	2	11	15.4
2	2	11	15.4
3	2	10	16.7
4	1	8	11.1
Averages	1.8	10	14.7
Control transect			
1	4	13	23.5
2	4	10	28.6
3	5	8	38.5
4	6	13	31.6
Averages	4.8	11	30.6
t-values	4.245*	0.632	4.940*
	$t_{0.05,(2),3} = 3.182$		

These results suggest that cryptogamic covers are less damaged by early winter grazing than by grazing at the same intensities but in late winter. Freedom from grazing in the late winter and spring while soil moisture is likely to be adequate to permit some regrowth of cryptogams may result in enough surface stabilization to significantly reduce runoff and sediment losses due to torrential summer rains. It also appears that avoidance of late winter grazing use permits a small increase in cryptogamic species richness.

The results suggest that desert ranges in areas where late winter and early summer rainfall is low and/or torrential when it does occur will suffer depletion of cryptogamic covers when heavy grazing is permitted to continue into the late winter. Lusby (1979) has demonstrated that in western Colorado early winter grazing results in less runoff and erosion than winter-long (to 15 May) grazing at the same intensity of use. Thus, avoidance of late winter use of desert ranges on the Colorado Plateau and in the Great Basin may reduce runoff and sedimentation downstream and prolong the useful life of large reservoirs, their hydroelectric plants, and other associated values. Cryptogamic crusts have the potential of slowing soil erosion by both wind and water, enhancing infiltration of precipitation, and stimulating vascular plant growth through improved soil water and available nitrogen relations.

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SIZE AND OVERLAP OF TOWNSEND GROUND SQUIRREL HOME RANGES

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Abstract.—We evaluated movement distance (an index of home range size) based on capture histories of 32 postbreeding Townsend ground squirrels (*Spermophilus townsendii*) on a 15 × 15 trap grid in southwestern Idaho. Capture frequencies and movement distances of adult males were significantly greater than those of other sex/age groups. Members of the same sex/age group were rarely captured at the same grid location, evidence of mutual avoidance within sex/age groups. These results are compared with those for other species of ground squirrels.

Ground squirrels offer favorable opportunities to investigate space use because of their abundance, relative ease of capture, and diel pattern of activity. Conversely, some populations demonstrate temporal differences in movement patterns related to sexual activity, food availability, density, dispersal, and interspecific competition. Thus, comparisons between congeners or even intraspecific populations require caution. In this study we evaluate indices of home range size of Townsend ground squirrels in the Birds of Prey Area in southwestern Idaho during the postbreeding season when home ranges were assumed to be stabilized.

Methods

In 1983 we established a 280 × 280-m grid of 225 Pymatuning live traps (Tryon and Snyder 1973) with 20-m spacing in a stand of big sagebrush (*Artemisia tridentata*) and winterfat (*Cerratoides lanata*). The grid incorporated Site 5 of Smith and Johnson (1985). Traps were baited with apple and opened during daylight hours 1–3 days per week between 15 February and 30 April, a total of 19 days.

Captured animals were toe-clipped, weighed, and immediately released. Because trapping had been conducted at this site annually since 1975, the ages of residents first marked as juveniles were known. We classified unmarked squirrels when first captured as juveniles, yearlings, adults, or unknown (at least one year of age) using the criteria of Smith and Johnson (1985). Capture records of juveniles (young of the year) and those in which > 50% of the captures occurred on the grid edge were eliminated from the analysis. We also eliminated capture histories that did not contain at least four grid locations, assuming that these inadequately sampled space use. Five movements (involving three animals) > 200 m were thought to be exploratory and were ignored in our calculations.

Analysis of movement distances assumes independence of capture locations (Swihart and Slade 1985). Serial dependence results in biased estimates of movement distance depending upon the pattern of captures. We used the microversion of the HOMERANGE computer program (Samuel et al. 1985) to calculate T2/R2, a test for independence in capture locations. Because 21 of 32 capture histories lacked independence in locations, we evaluated capture data of sex/age groups rather than individuals to minimize the effects of autocorrelation. There was no significant difference ($P < .13$) in successive movement distances recorded during the same day and those separated by more than 24 hrs. Thus, serial dependence was due to the pattern of spacial use rather than insufficient time between successive captures (Swihart and Slade 1987).

We calculated (1) DS, the mean distance between successive captures, as d_i/m_i where d_i is the cumulative linear distance between successive capture locations and m_i is the number of movements for squirrels of sex/age group *i*, and, (2) AD (Koeppl et al. 1977), the mean distance between all capture locations as $d_i/[\Sigma\, n_i\, (n_i - 1)/2]$ where d_i is the cumulative linear distance between all capture locations

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TABLE 1. Mean capture frequency and movement distance (± SE) in m of Townsend ground squirrels: DS, mean distance between successive captures, and AD, mean distance between all capture locations. Sample size in parentheses. * = significant difference ($P < .05$) from other sex/age groups. ** = significant difference between sexes.

Sex/age	No. captures	DS	AD
Ad males	19.1 ± 2.0 (191)*	28.6 ± 1.3 (181)*	38.7 ± 2.9 (327)*
Yr males	8.1 ± 1.0 (58)	26.9 ± 4.4 (51)	31.4 ± 3.4 (54)
Ad females	9.5 ± 2.7 (66)	23.0 ± 2.4 (58)	35.4 ± 2.7 (57)
Yr females	11.0 ± 1.9 (76)	25.3 ± 2.0 (70)	35.5 ± 3.2 (96)
All males	14.6 ± 1.8 (249)**	28.2 ± 1.4 (232)	37.7 ± 0.9 (381)**
All females	10.3 ± 1.7 (142)	24.3 ± 1.5 (128)	35.4 ± 1.5 (153)
All animals	12.2 ± 1.2 (391)	26.8 ± 3.8 (360)	37.0 ± 3.0 (534)

TABLE 2. Overlap (%) of capture locations among sex/age groups. * = significant difference ($P < .03$) from cells involving unlike sex/age groups.

Traps capturing	Also capturing			
	Ad males	Yr males	Ad females	Yr females
Ad males	8*	23	17	22
Yr males	50	3*	13	20
Ad females	45	16	6*	26
Yr females	57	17	23	11*

and n_i is the number of locations of squirrels within a sex/age group i.

RESULTS

Of the 146 squirrels captured, the capture histories of 32 animals one or more years of age (17 males and 15 females) met the criteria established for spacial use analysis.

The mean capture frequency of adult males was significantly greater ($F = 2.6$; $P < .05$) than that of other sex/age groups (Table 1). Both measures of movement distance were significantly greater for adult males than other sex/age groups (DS: $F = 3.59$, $P < .02$; AD: $F = 5.83$, $P < .001$). Of these three variables, capture frequency and AD were significantly different ($F = 5.4$, $P < .03$ and $F = 6.2$, $P < .02$, respectively) between the sexes (Table 1).

The mean distance between centers of activity of 11 adults (7 males, 4 females) in successive years (1982 and 1983) was 52 ± 11 m (range 12 to 131 m), similar to that of adult Columbian ground squirrels (*Spermophilus columbianus*) (Murie and Harris 1984).

Home range overlap was measured as the percentage of capture stations at which members of the same or different sex/age groups were also taken. Overlap was significantly less frequent among members of the same sex/age group than among different groups ($F = 6.7$, $P < .03$, Table 2). Differences in the mean and total number of capture locations among sex/age groups produced asymmetries in home range overlaps. For example, yearling males occurred at 23% of the stations at which adult males were captured, but adult males occurred at 50% of the stations at which yearling males were captured (Table 2).

DISCUSSION

Home range sizes of postbreeding ground squirrels may or may not differ between the sexes (Owings et al. 1977, Michener 1979). In our study home ranges of adult males were significantly larger than those of other sex/age groups (Table 1). Postbreeding males were also more mobile and prone to capture. It is likely that the difference in home range size between the sexes is increased during the breeding season when adult males search for females in estrus (Murie and Harris 1978, Michener 1979).

Spacing in ground squirrel populations reflects social status and in some cases kinship (Michener 1979). In our study overlap in space use by members of the same sex/age group was rare in comparison with that by members of different groups (Table 2). Squirrels clearly avoided trap locations used by individuals of the same sex and age. Using direct observation, Michener (1979) found that adult Richardson ground squirrels (*Spermophilus richardsoni*) of the same sex maintained greater distances when simultaneously active aboveground than distances between their centers of activity, another example of mutual avoidance. However, there was extensive overlap in the home ranges of both adult females and adult males. We found that overlap in space use by yearling and adult females was no more frequent than that of other sex/age combinations (Table 2). Thus, we are uncertain if female offspring are likely to take up residency near their mothers as observed in Richardson ground squirrels (Michener 1979).

In summary, the home range characteristics of postbreeding Townsend ground squirrels are similar to those of certain other species of the genus *Spermophilus*. Adult males occupy larger home ranges than those of other sex/age groups. There is significantly less overlap in space use by members of the same sex/age group than those of different groups.

ACKNOWLEDGMENTS

We thank Karen Steenhof and an anonymous reviewer for comments that significantly improved the manuscript. Tim Reynolds and his students at Boise State University provided field assistance. Fred Leban provided guidance regarding data analysis. We thank Michael Kochert, research leader, Snake River Birds of Prey Area, for encouragement and cooperation. This work was part of the USDI, Bureau of Land Management, Snake River Birds of Prey Research Project, funded under contract 52500-CT5-1002 to the University of Idaho.

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PISOLITHUS TINCTORIUS, A GASTEROMYCETE, ASSOCIATED WITH JEFFREY AND SIERRA LODGEPOLE PINE ON ACID MINE SPOILS IN THE SIERRA NEVADA

R. F. Walker[1]

ABSTRACT.—Basidiocarps of *Pisolithus tinctorius*, a gasteromycetous fungus adapted to harsh sites, were observed in association with Jeffrey and Sierra lodgepole pine on acid mine spoils in northeastern California. Subterranean mycelial strands were traced from these basidiocarps to the root systems of the two pine species, which had ectomycorrhizae characteristic of those formed by this fungus in symbiotic relationships with conifer hosts.

The ectomycorrhizal fungus *Pisolithus tinctorius* (Pers.) Coker & Couch occurs essentially worldwide in temperate, subtropical, and tropical zones and in symbiotic association with a wide variety of conifer and hardwood hosts (Marx 1977). In the United States its basidiocarps have most frequently been observed on harsh sites in the East, South, and Midwest associated with various pine species (Lampky and Peterson 1963, Schramm 1966, Hile and Hennen 1969, Lampky and Lampky 1973, Marx 1975). Prompted by these reports of the ability of this Gasteromycete to flourish on infertile and often toxic substrates, researchers have inoculated several southern pine species in forest nurseries with this mycobiont (Marx et al. 1984). Their efforts have resulted in substantial improvement in seedling performance upon outplanting on a variety of adverse sites (Berry and Marx 1978, Marx and Artman 1979, Walker et al. 1985). Current research efforts include identification of new tree hosts for inoculation trials and development of more effective inocula incorporating locally adapted *P. tinctorius* isolates.

Numerous basidiocarps of *P. tinctorius* were observed on spoils of the Leviathan Mine in Alpine County, California (38°42′30″N, 119°39′15″W), in mid-September 1988. This open-pit sulfur mine consists of approximately 100 ha at an elevation of 2,200 m and receives an average annual precipitation of about 50 cm, primarily as snowfall. Early attempts to revegetate the mine, inactive since 1962, failed. More recent efforts using woody and herbaceous species were somewhat successful, and limited natural vegetation, comprised largely of woody species, has become reestablished near adjoining undisturbed forest and woodland. Nevertheless, vegetative cover is sparse over most of the site. A comprehensive examination of soil chemical properties by Butterfield and Tueller (1980) revealed that most of these spoils have a pH of 4.0 to 4.5, a deficiency of plant-available N, and potentially phytotoxic concentrations of Al.

A majority of the *P. tinctorius* basidiocarps observed were in close proximity to seedlings and saplings of Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), resulting from both earlier plantings and natural colonization of the mine spoils. Fewer basidiocarps were found near naturally invading seedlings and saplings of Sierra lodgepole pine (*Pinus contorta* var. *murrayana* [Grev. & Balf.] Engelm.). California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.) and occasional singleleaf pinyon (*Pinus monophylla* Torr. & Frem.), Utah juniper (*Juniperus osteosperma* [Torr.] Little), and quaking aspen (*Populus tremuloides* Michx.) were also found growing in the mine, but no basidiocarps were observed in the immediate vicinity of any of these four species.

These basidiocarps, dark yellow to brown in color, matched the description of Coker and Couch (1928) for *P. tinctorius*, which is very distinctive due to the presence of peridioles in the upper portion of the gleba. Specimens examined on this site included those of the stipitate, substipitate, and sessile forms, which varied in size from 8 to 21 cm in height and from 3.5 to 8 cm in diameter. As many as five basidiocarps were observed encircling solitary Jeffrey pines, but no more than three were observed around isolated lodgepole pines. Clusters of either species tended to be accompanied by large numbers of basidiocarps, the total of which numbered several hundred over the entire site.

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Removal of the soil from around individual basidiocarps exposed mycelial strands that were traced up to 1.5 m through spoil materials to root systems of both Jeffrey and lodgepole pine. With gold-yellow pigmentation, these mycelial strands compared favorably with the description of *P. tinctorius* rhizomorphs provided by Schramm (1966) and were joined at the root systems of both tree species with ectomycorrhizae closely resembling those Marx and Bryan (1975) identified as formed by this mycobiont. Subsequently, it is reasonable to conclude that the ectomycorrhizal root systems of Jeffrey and Sierra lodgepole pine on this site resulted from a symbiotic association with *P. tinctorius*.

ACKNOWLEDGMENTS

This paper contains results of the Nevada Agricultural Experiment Station Research Project 619 funded by the McIntire-Stennis Cooperative Forestry Research Program. The author is indebted to P. M. Murphy of the Division of Forestry, Nevada Department of Conservation and Natural Resources, and to D. C. Prusso of the Department of Biology, University of Nevada, Reno, for their invaluable assistance.

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SPATIAL AND TEMPORAL VARIABILITY IN PERENNIAL AND ANNUAL VEGETATION AT CHACO CANYON, NEW MEXICO

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ABSTRACT.—Annual plant populations in northwestern New Mexico were found to be spatially and temporally highly variable. During favorable years annual plant species have patterns of dominance and diversity that are different from those of perennial species. Measurement of perennial plant diversity in plant communities is a poor predictor of productivity. Both perennial and annual components of plant communities should be considered in measurements of diversity and productivity.

The relationship between environmental diversity and animal populations is of interest to ecologists in their attempts to understand the factors that control the composition of biotic communities (Pielou 1974). Whitaker (1972) and Pielou (1974) discuss two different types of diversity. Alpha diversity is applied to small, homogeneous areas such as local plant communities or habitat types, defined by more or less natural boundaries. Beta diversity is the measurement of differences between these small, homogeneous areas within a geographic region.

Perennial plant species are often used in descriptive and quantitative studies of plant communities that include measurements of dominance and diversity. While perennial plants are the relatively more stable part of the plant community, annual plant species are a conspicuous component during years when environmental conditions are right for germination, growth, and reproduction. The fluctuation of annual plant populations has been studied in several arid and semiarid locations in the southwestern United States (Beatley 1969, Juhren et al. 1956, Patten 1978, Tevis 1958). In desert and semiarid ecosystems, annual plant production is characterized by a fascinating cycle of years of low germination interspersed with years of superabundant germination and reproduction. This production may be a significant resource for consumer populations, but it may also be overlooked by researchers because of the high degree of variability from year to year.

In this study we report on work done at Chaco Canyon, in northwestern New Mexico. Our work included measurements of perennial species to describe habitat types and their alpha diversity. In addition, we documented one superabundant year of annual plant production, followed by several consecutive years of little or no annual production. In northwestern New Mexico fluctuation in annual plant populations has been described (Jones 1972, Potter 1974, Scott 1980), but quantitative data have not been reported.

STUDY AREAS

Chaco Canyon is in the central San Juan Basin in northwestern New Mexico. The San Juan Basin is an extension of the Colorado River drainage, although the Chihuahuan Desert to the south influences the climate and the composition of the vegetation. The soils are generally derived from shale and sandstone. The vegetation is dominated by members of the Asteraceae and Chenopodiaceae, including sagebrush (*Artemisia*), rabbitbrush (*Chrysothamnus*), and various saltbushes (*Atriplex*) (Donart et al. 1978, Shreve 1942). As in the Great Basin to the west, winter precipitation is a significant component of the total in northwestern New Mexico, but the summer monsoonal rains from the south provide a large proportion of the rainfall during the growing season (Tuan et al. 1973). A summary of weather data at Chaco Canyon over a 20-year period, 1957–1977 (Cully

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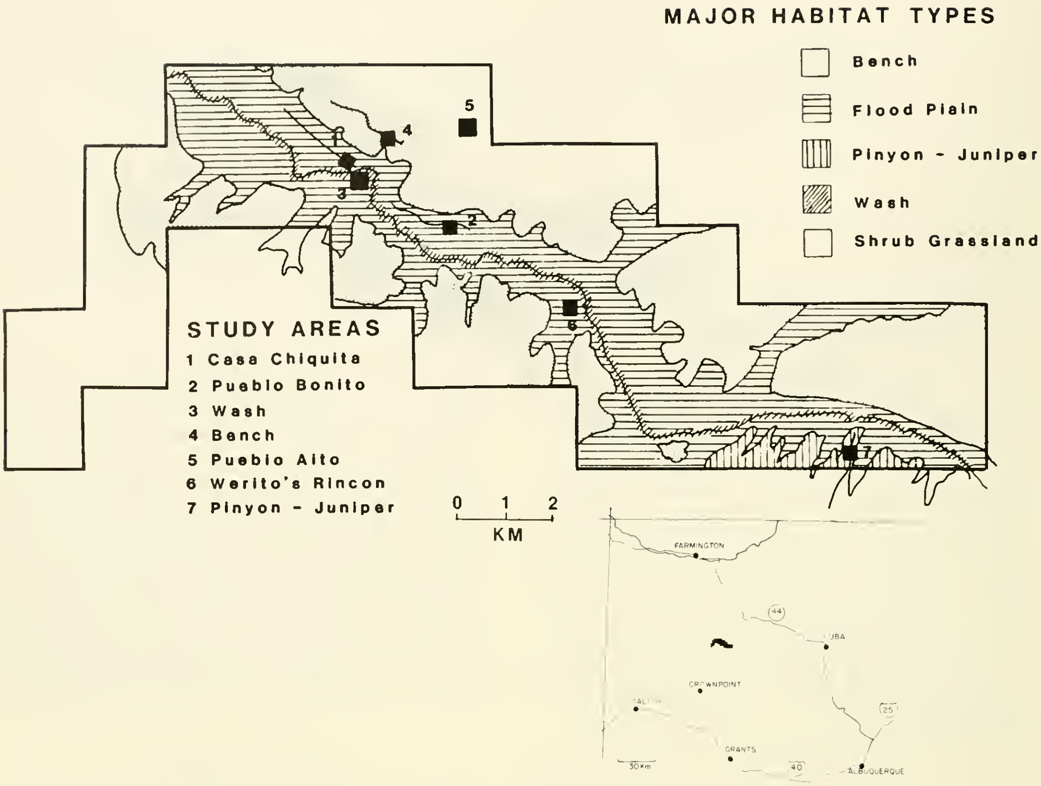
MAJOR HABITAT TYPES
Bench
Flood Plain
Pinyon - Juniper
Wash
Shrub Grassland
STUDY AREAS
1 Casa Chiquita
2 Pueblo Bonito
3 Wash
4 Bench
5 Pueblo Alto
6 Werito's Rincon
7 Pinyon - Juniper
0 1 2
KM
FARMINGTON
44
CROWNPOINT
GRANTS
25
40
ALBUQUERQUE
30km

Fig. 1. Map of Chaco Canyon showing the locations of the study sites and the distribution of vegetation types.

1984b), showed that annual precipitation averaged 20.6 cm. The heaviest precipitation occurred during July through September, with each of these months averaging >3 cm. The balance of the rainfall was rather evenly distributed throughout the remainder of the year. The San Juan Basin can have two periods of plant productivity, one in spring if there is normal or above normal precipitation, and another more predictable period during late summer and fall in response to the monsoonal rains of late summer.

The study sites for this report are five areas used by J. Cully (1984a) in his study of the bird and rodent communities of the San Juan Basin. They were selected from Kelley and Potter's (1974) vegetation map of Chaco Canyon. The principal criteria for the choices were that each area included habitat sufficient to contain a transect 120 m wide by 1.6 km long, that the areas were different from one another, and that in combination they represented the major habitats at Chaco Canyon. The sites at Pueblo Alto and at the mouth of Werito's Rincon were added for this study to gather additional data on annual plant productivity.

Upland Areas

THE BENCH.—The bench lies within the *Hilaria-Bouteloua-Atriplex* vegetation type (Kelley and Potter 1974). The bench (Fig. 1) is elevated above the floodplain of the Chaco Wash and is bounded on the north and south by sandstone cliffs. Soils are thin, and there is a great deal of exposed bedrock.

PINYON-JUNIPER.—The woodlands of the higher elevations of Chacra Mesa are dominated by one-seed juniper (*Juniperus monosperma*). Pinyon pine (*Pinus edulis*) is subdominant.

PUEBLO ALTO.—Pueblo Alto is located in a shrub grassland, the *Atriplex-Oryzopsis-Sporobolus* vegetation type (Kelley and Potter 1974). The site is located on the mesa north of the canyon proper.

Floodplain Areas

CASA CHIQUITA AND PUEBLO BONITO.—Two study sites lie within the *Atriplex-Sarcobatus* vegetation type in the floodplain of the wash, which is dominated in the western portion of Chaco Canyon by four-wing saltbush, shadscale, and black greasewood (Kelley and Potter 1974). The sites are bordered on the south by the wash and on the north by sandstone cliffs and the bench habitat.

THE WASH.—The wash is the erosion channel of the Chaco River. It bisects the floodplain through the length of the canyon in the park. Riparian, woody vegetation is characteristic of the wash habitat; the inner channel is dominated by rabbitbrush (*Chrysothamnus nauseosus*), sandbar willow (*Salix exigua*), and black greasewood (*Sarcobatus vermiculatus*). Cottonwood (*Populus fremontii*), four-wing saltbush (*Atriplex canescens*), and tamarisk (*Tamarix* spp.) also occur.

WERITO'S RINCON.—This study site is at the mouth of a large rincon, or side canyon, southwest of the main canyon. According to Kelley and Potter (1974), the vegetation is similar to that on the mesa tops surrounding the Pueblo Alto study area.

METHODS

Perennial plant cover was measured using the line intercept method (Canfield 1941). Cover was measured on twenty-five 10-m lines stretched in alternate directions at 62-m intervals along a 1.6-km transect in each habitat. This yielded a total of 250 m sampled in each habitat. Each perennial plant species intercepted was measured to the nearest cm. The bench, Casa Chiquita, and the wash were sampled during April 1979. Pueblo Bonito and the pinyon-juniper sites were sampled during May 1981.

To identify the species that most easily distinguish habitats, we applied discriminant function analysis to the cover data from each 10-m line segment in each habitat. The habitats were the discriminating variables, and the 29 species of plants that were encountered on three or more (of a total of 125 segments) were the predictor variables. This analysis was done on a microcomputer using SPSSPC+ Advanced Statistics (Norusis 1986).

The cover data at each transect were analyzed for species richness, or S (number of species) = H_0; two indices of species diversity, $1/\Sigma p_i^2 = H_1$ (Simpson 1949) and $\exp(-\Sigma p_i \ln p_i) = H_2$ (Shannon and Weaver 1949); and evenness, or J, where $J = H_2/H_0$ (Peet 1974, Pielou 1974). Hill (1973) suggests that evenness as measured above is subject to change with change in sample size, and that the ratio H_1/H_0 is a better ratio to describe evenness. This is partly because H_2 always lies between H_0 and H_1. Since J is still common in the literature, we present both measures of evenness.

Annual plant densities were sampled at the bench, Casa Chiquita, Pueblo Bonito, and Pueblo Alto in June 1979, 1980, and 1981, and at Werito's Rincon during June 1979. At each area data were taken from twenty 1/2-m^2 quadrats. These were placed at 10-m intervals along 100-m tapes laid at random in a 1-ha area along the transect used to measure cover at Casa Chiquita, Pueblo Bonito, and the bench. Cover was not measured at Pueblo Alto or at the mouth of Werito's Rincon; a transect was laid out in the same way at these two sites as at the previous sites to gather the annual data. The number of annual plants within each quadrat was counted by species. Then all vegetation was picked and saved in plastic bags to determine the aboveground biomass production. The plant material was air-dried at room temperature for a minimum of two months. Each sample was weighed to the nearest 0.1 g. Subsequently, the seeds were removed from foliage, stems, and flower parts in a seed separator and weighed separately.

RESULTS

Perennial Plant Species Dominance

In the upland areas the dominant species on the bench were Mormon tea (*Ephedra viridis*), Bigelow's sagebrush (*Artemisia biglovii*), wild buckwheat (*Eriogonum* spp.), Greene's rabbitbrush (*Chrysothamnus greenei*), galleta grass (*Hilaria jamesii*), and Indian ricegrass (*Oryzopsis hymenoides*) (Table 1). The pinyon-juniper habitat on Chacra Mesa was dominated by Bigelow's sagebrush, mountain mahogany (*Cercocarpus montanus*), three-leaf sumac (*Rhus trilobata*), pinyon pine, one-seed juniper, and galleta grass. On the floodplain the dominant species at Casa Chiquita were broadscale (*Atriplex obovata*), black greasewood, torrey seepweed (*Sueda torrey-*

TABLE 1. Cover and diversity at five habitats at Chaco Canyon. The values are the number of cm intercepted for each species at twenty-five 10-m lines in each habitat. H_0 = number of species; $H_1 = 1/P_i^2$; $H_2 = -\Sigma P_i \mathrm{Ln} P_i$; $J = H_2/H_0$; evenness = H_1/H_0.

Species	Bench	Casa Chiquita	Pueblo Bonito	Wash	Pinyon-juniper
Agropyron spp.	0	0	0	71	0
Aristida spp.	0	0	0	0	17
Artemisia bigelovii	1195	0	0	0	665
Artemisia dracunculoides	0	0	0	190	0
Artemisia tridentata	0	0	0	573	51
Astragalus spp.	0	0	0	0	34
Atriplex canescens	64	187	3829	0	0
Atriplex obovata	0	1808	0	0	0
Bouteloua gracilis	0	0	0	0	80
Cercocarpus montanus	0	0	0	0	376
Chrysopsis villosus	27	0	0	0	0
Chrysothamnus greenei	200	0	0	0	0
Chrysothamnus nauseosus	0	0	0	2953	100
Chrysothamnus pulchellus	107	0	0	0	0
Ephedra viridis	680	0	0	0	23
Eriogonum spp.	516	0	0	0	11
Eurotia lanata	49	0	0	0	83
Fallugia paradoxa	0	0	0	0	95
Gutierrezia sarothrae	10	0	21	0	100
Hilaria jamesii	327	0	325	0	181
Juniperus monosperma	0	0	0	0	2117
Lycium pallidum	0	0	44	0	29
Muhlenbergia pungens	92	0	0	0	0
Opuntia spp.	6	0	0	0	18
Oryzopsis hymenoides	324	0	4	80	10
Other	24	0	0	151	23
Pinus edulis	0	0	0	0	317
Populus fremontii	0	0	0	200	0
Rhus trilobata	79	0	0	0	217
Salix spp.	0	0	0	1772	0
Sarcobatus vermiculatus	0	1215	2260	0	0
Sporobolus airoides	0	765	131	309	0
Sporobolus spp.	101	0	0	0	0
Sueda torreyana	0	286	202	0	0
Tamarix pentandra	0	0	0	2197	0
Yucca spp.	51	0	0	0	35
Total cover	3952	4261	6816	8496	4582
% cover	16%	17%	27%	34%	18%
H_0	17	5	8	10	21
H_1	6.30	3.33	2.33	4.19	3.96
H_2	2.18	1.35	1.07	1.68	1.97
J	0.13	0.27	0.13	0.17	0.09
Evenness	0.37	0.67	0.21	0.41	0.19

ana), and alkali sacaton (*Sporobolus airoides*). Pueblo Bonito was similar to Casa Chiquita, except that broadscale was missing and fourwing saltbush was much more important than at Casa Chiquita. Black greasewood and seepweed were also important at Pueblo Bonito. Galleta grass was absent at Casa Chiquita but contributed 2% cover at Pueblo Bonito. The wash was dominated by rabbitbrush, tamarisk, sandbar willow, and big sagebrush. Shrubs and forbs were the primary components of the vegetation at all study sites sampled for perennial vegetation.

In the discriminant function analysis there were 12 species important in discriminating between the habitats (Table 2). The list includes many of the species listed above as dominants plus *Artemisia dracunculoides*. Although galleta, wild buckwheat, mountain mahogany, three-leaf sumac, Torrey seepweed, big sagebrush, and sandbar willow were all subdominant in one or more habitats,

TABLE 2. List of species used by the discriminant function analysis and the univariate F value in a oneway analysis of variance of each species for differences between habitats. All values are significant at P < .001.

	Species	F to enter
1	*Atriplex obovata*	27.04
2	*Atriplex canescens*	16.75
3	*Artemisia bigelovii*	15.68
4	*Chrysothamnus nauseosus*	14.92
5	*Tamarix pentandra*	8.23
6	*Oryzopsis hymenoides*	8.06
7	*Sarcobatus vermiculatus*	7.57
8	*Chrysothamnus greenii*	7.47
9	*Ephedra viridis*	7.43
10	*Sporobolus airoides*	7.42
11	*Juniperus monosperma*	6.89
12	*Artemisia dracunculoides*	6.66

they were not used by the DFA. This may be partly due to the high probability level required for inclusion with 27 variables (P < .002; .05/27). Figure 2 shows the relationships of the observations from each habitat on canonical variables (discriminant function axes) 1 and 2. Casa Chiquita and Pueblo Bonito are similar to each other. The bench and pinyon-juniper habitats are also very similar; in fact, they are almost completely overlapping on canonical axes 1 and 2. (They are separated on axis 4 where juniper is an important variable.) The wash habitat was distinct from the others with a small area of overlap on canonical axes 1 and 2.

One value of the DFA is the ability to show which habitats are most similar to each other and, by a jackknife procedure, to show how accurately the habitats can be distinguished on the basis of the predictor variables. The jackknife procedure takes each of the observations used to derive the discriminant functions and tests, *a posteriori*, the accuracy with which the cases are attributed to the correct groups; it is a test of the accuracy of the discriminant functions to discriminate between groups.

At all habitats the DFA correctly assigned 80% or more of the samples. At the bench two samples were misclassified to pinyon-juniper, and at the pinyon-juniper two were misclassified to the bench. These two habitats are broadly overlapping on DF axes 1 and 2

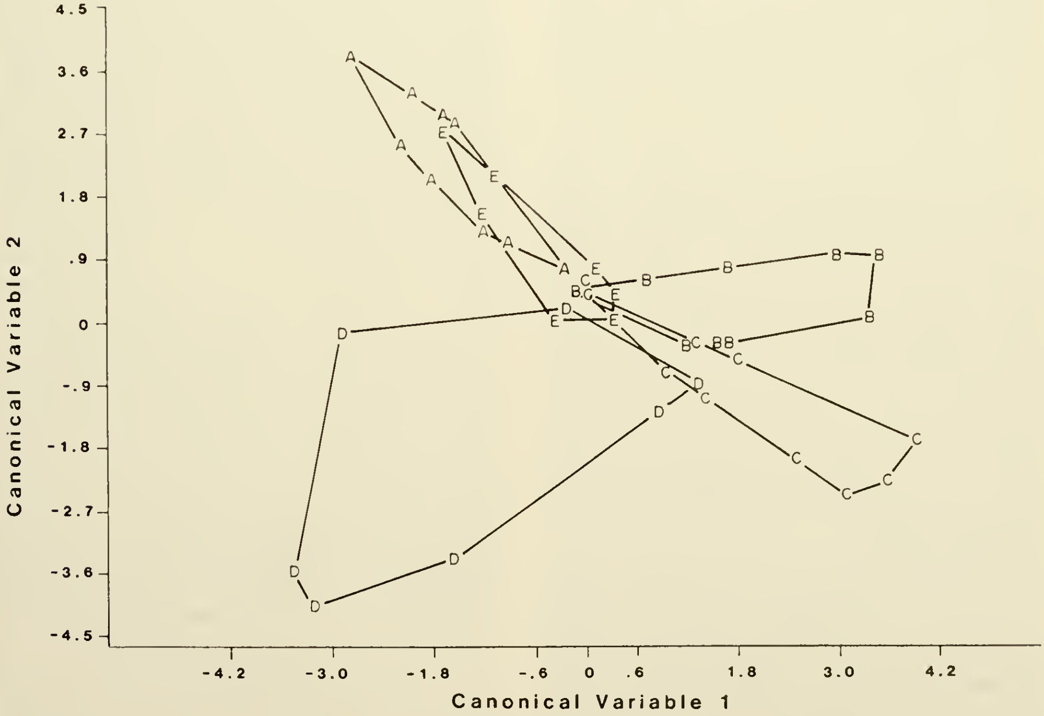

Fig. 2. Relationship of each habitat based on discriminant function analysis of perennial vegetation on the first two discriminant function axes (canonical variables), which account for 65% of the vegetative variance. A = bench, B = Casa Chiquita, C = Pueblo Bonito, D = wash, and E = pinyon-juniper.

TABLE 3. Results of the discriminant function analysis bootstrap analysis to determine the accuracy of classifying cover samples to their correct habitats. See text for explanation.

		Number of cases classified into group				
Group	% correct	Bench	Casa Chiquita	Pueblo Bonito	Wash	Pinyon-juniper
Bench	92	23	0	0	0	2
Casa Chiquita	80	0	20	4	0	1
Pueblo Bonito	88	0	1	22	0	2
Wash	80	0	0	2	20	3
Pinyon-juniper	92	2	0	0	0	23
Total		25	21	28	20	31

(Fig. 2). They are also similar in species composition, species richness, and cover (Table 1). Casa Chiquita and Pueblo Bonito were classified by Kelley and Potter (1974) as belonging to the same habitat type; thus, it is not surprising that four samples from Casa Chiquita were misclassified to Pueblo Bonito and one from Pueblo Bonito was misclassified to Casa Chiquita. The perennial vegetation at Pueblo Bonito was more variable than that at Casa Chiquita, and two samples were misclassified to the pinyon-juniper, which shared four species with Pueblo Bonito. The wash was the most variable habitat on DF axes 1 and 2 and had three samples misclassified to pinyon-juniper and two to Pueblo Bonito.

Perennial Plant Species Diversity and Cover

The bench had the second highest species richness and the highest diversity according to the two diversity indices (Table 1). It also had the lowest cover of the five habitats. The pinyon-juniper habitat was similar to the bench in its high species diversity, particularly richness, and low cover values. On the floodplain, Casa Chiquita had considerably lower diversity than the bench, but cover that was similar in value. Pueblo Bonito had similar diversity to Casa Chiquita, but much higher cover. The wash had similar cover, but greater diversity.

Annual Plant Species Density and Diversity

At all five areas sampled for annual plant densities the total densities were considerably higher in 1979 than in the following two years (Table 4). Annual species richness was also higher during 1979, with most species occurring only in that year. The densities varied considerably from site to site, the floodplain sites producing higher annual densities than the upland locations.

The annual species composition at Werito's Rincon was different from the other sites (Table 4, Fig. 3). In 1979 pinnate tansy-mustard (*Descurainia pinnata*) was the dominant annual in terms of density at all sampling locations except Werito's Rincon. There, stickleaf (*Mentzelia* spp.) was the most abundant.

Biomass Measures

At the floodplain sites of Casa Chiquita and Pueblo Bonito the high annual plant densities were accompanied by high biomass in 1979 (Table 5, Fig. 4). At Werito's Rincon, in spite of densities similar to those at Casa Chiquita, the total biomass and seed biomass were much lower in 1979. The differences between these study areas in biomass may have been related to the differences in species composition of the annual populations at the two sites or to local differences in soil conditions and water availability. Overall, the flood plain sites were more productive than the upland sites during 1979. Biomass was drastically reduced at Casa Chiquita and Pueblo Bonito in 1980. However, at the upland sites of Pueblo Alto and the bench, total plant biomass and seed biomass were higher than in 1979. The biomass figures include grasses, a component of the perennial vegetation whose growth and reproduction may not be affected by winter-spring moisture until later in the same year or the following year. Biomass was low at all sites in 1981.

DISCUSSION

Because perennial plant species are relatively stable components of the plant community, measurements of their characteristics

Table 4. Annual plant densities at Chaco Canyon (no./m^2).

	Casa Chiquita			Pueblo Bonito			Bench			Pueblo Alto			Werito's Rincon
	1979	1980	1981	1979	1980	1981	1979	1980	1981	1979	1980	1981	1979
Astragalus	0	0	1.6	0	0	0	2.7	2.7	1.6	11.9	0	0	4.7
Atriplex	0	0.1	0	5.7	0	0	0	0	0	0	0.2	0	0
Chenopodium	0.2	0	0.1	1.4	0	0	0	0	0	0.2	0	0	0
Cryptantha	23.3	0	0	15.8	0	0.2	0.2	0.1	0	18.6	0	0	1.5
Descurainia	144.3	0	0	45.1	0	0	7.1	0	0	41.1	0	0	29.1
Ipomopsis	0.4	0	0	0	0	0	0	0	0	0	0	0	0.6
Lappula	1.0	0	0	3.7	0.2	0	0.4	0	0	0.2	0	0	0.1
Mentzelia	0	0.3	0	0	0	0	0	0	0	0.5	1.5	0	96.1
Phacelia	0	0	0	0.2	0	0	1.4	0	0	3.7	0	0	0
Plantago	0	0	0	0	0	0	0	0	0	3.5	0	0.1	49.5
Portulaca	0	0	0	1.4	0	0	0	0	0	0	0	0	0
Salsola	5.4	0	0	2.7	2.1	5.9	0	0	0	0.3	0	0	3.9
Senecio	0.4	0	0	0	0	0	0	0	0	2.3	0	0	16.3
Solanaceae	0.7	0	0	0.4	0	0	0	0	0	0	0	0	0
Sphaeralcea	0	0	0	0	0	0	0	0	0	0.2	0	0	8.1
Stephanomeria	0	0	0	0	0	0	0	0	0	0	0	0	2.3
Streptanthella	0	0	0	0	0	0	3.2	0	0	0.7	0	0	0
Townsendia	37.2	0	0	6.2	0	0	0	2.1	0	1.4	0.6	0	0
Other*	0	0	0	0.7	0.4	0.2	0.7	0	0.1	0.7	0.1	0	0.1
Unknown	7.1	0.3	0.1	1	0	0	1.2	0	0	0.9	0	0	10.6
Number sp. (richness)	10	3	3	12	3	3	8	3	2	15	4	1	13
Total density	220	0.7	1.8	84.3	2.7	6.3	16.9	4.9	1.7	86.2	2.4	0.1	222.9

*Other includes all identified species that never reached a density of 0.5 per m^2.

provide information that can be used to distinguish one habitat type from another. The results of this study indicate that the wash, the floodplain, the bench, and the mesa tops are distinct habitat types. Individual species distribution may overlap habitat types, but each type is distinguished either by the presence of species unique to that habitat or by the greater dominance of particular species over others.

One of the most conspicuous characteristics of annual plant productivity is the variability from year to year. Juhren et al. (1956) found that different constellations of annual species germinate under specific combinations of temperature and rainfall at Joshua Tree National Monument in southern California. During some years only a few individuals occurred. Likewise, in Nevada, Beatley (1969) observed that biomass of annual species fluctuated both spatially and temporally, depending on local conditions.

At Chaco Canyon annual spring plant densities fluctuated drastically from year to year during the period 1979–1981. We believe that the dramatic abundance of annuals in 1979 was due to late winter and spring precipitation that fell at Chaco Canyon in 1978–1979. During December and January mean monthly temperatures were low (Fig. 5), resulting in low water loss from soil and low evapotranspiration rates. These climatic conditions were favorable for the germination and growth of annuals to reproductive maturity. Conditions were particularly favorable for pinnate tansymustard, which, we believe (based on densities), accounts for most of the increase in total biomass and seed biomass on the study plots. However, perennial grasses also contributed to the total. Different climatic conditions produce different dominant species in the annual plant populations from year to year, and there are years when annual species are rare or absent. Another characteristic of annual production is spatial variability. Within a limited geographic area such as Chaco Canyon, the abundance and species composition of annual plant populations differ from habitat to habitat during the same growing season. Patten (1978) noted similar differences in productivity in annual plants in different microhabitats within a Sonoran Desert shrub community. During the winter and spring of 1978–1979 the climatic conditions were probably the overriding factors in the abundance of annuals throughout Chaco Canyon. The differences

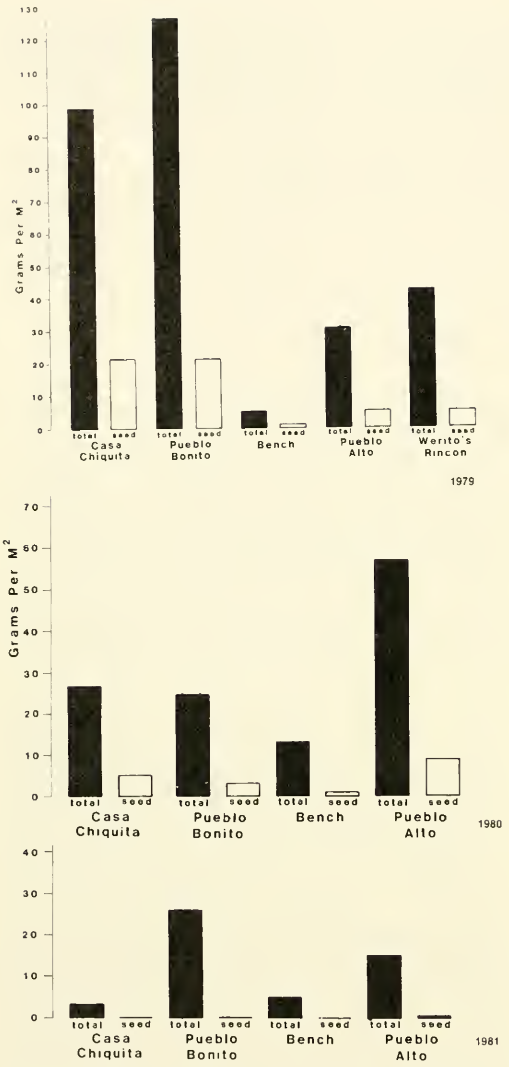

Fig. 3. Total plant and seed biomass at five sites at Chaco Canyon during three years.

in the species composition and the productivity between habitat types were probably a result of local characteristics of soil and physiography.

TABLE 5. Vegetation biomass of annual plants and grasses at five locations (g/m^2).

	Total plant biomass (5m^2)				
Location	Year	Mean	SE	Mean	SE
Casa Chiquita	1979*	98.8	12.68	21.8	2.52
	1980	28.6	6.93	4.6	1.12
	1981	3.8	0.97	0	0
Pueblo Bonito	1979	126.8	9.65	20.56	1.82
	1980	24.26	5.02	2.9	0.55
	1981	26.18	4.26	0	0
Bench	1979	5.52	0.88	0.74	0.12
	1980	13.46	2.12	1.98	0.32
	1981	5.08	0.74	0	0
Pueblo Alto	1979	32.50	2.27	5.44	0.53
	1980	57.46	4.51	8.84	0.75
	1981	15.94	1.29	4.72	0.45
Werito's Rincon	1979	42.34	2.91	4.72	0.45

*We collected biomass samples from only 10 plots at Casa Chiquita in 1979.

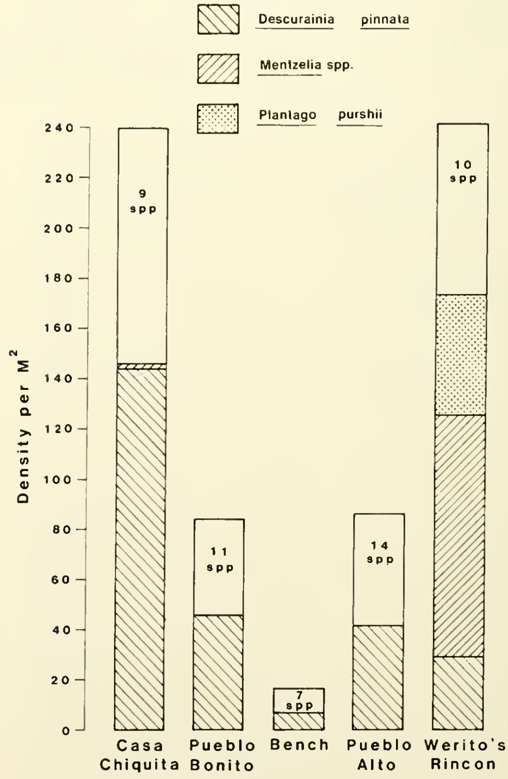

Fig. 4. Total density and density of dominant annual species from five sites at Chaco Canyon in 1979.

SUMMARY

We measured attributes of both perennial and annual plant species in four habitat types at Chaco Canyon. These habitat types were found to be distinct, based on perennial species representation and/or relative dominance of perennial species. Diversity based on perennial species was higher on the bench and in the wash, and the lowest by all measures of diversity at Pueblo Bonito.

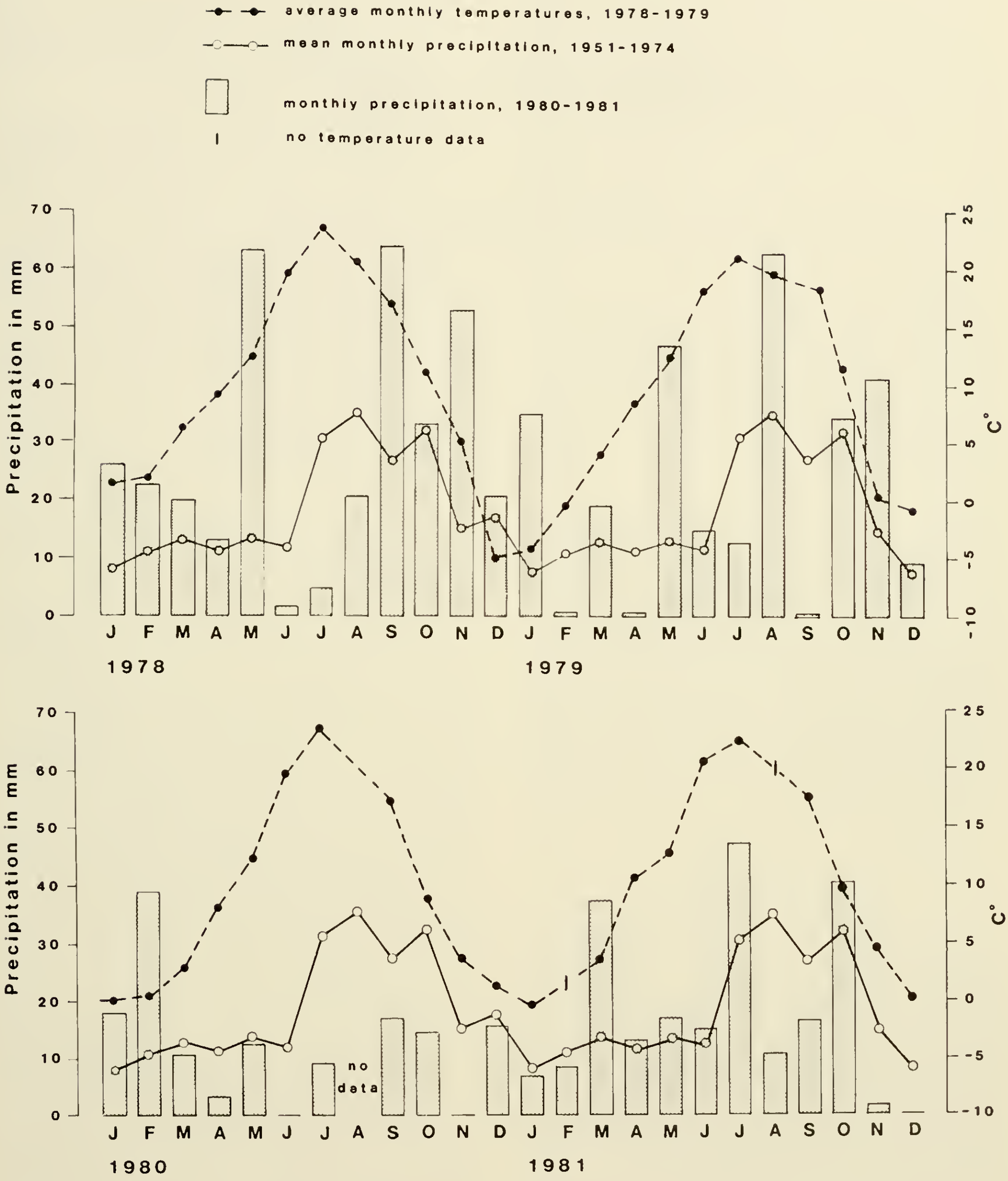

Fig. 5. Monthly precipitation during the study and 20-year mean temperature and precipitation at Chaco Canyon.

At Chaco Canyon annual plant species are an important component of the plant community even though their appearance is highly variable both spatially and temporally. Annual plant species occurred in all habitat types in varying densities and profoundly affected the aboveground biomass from place to place and from year to year. Annual plant species density, diversity, and biomass were high on the floodplain sites during 1979 but low during the other two years. Annual plants on the bench had the lowest production measured during 1979, when the floodplain sites were producing at their peak. Annual plant density at Pueblo Alto and Werito's Rincon was also high during 1979; however, the greatest biomass at Pueblo Alto was measured in 1980, during the year following the wet winter-spring of 1978–1979. This apparently reflects the development of grasses that responded to the wet period more slowly than annual plants. Thus, while the floodplain habitats were the most productive during exceptionally wet years, the upland habitats appeared to be more productive during drier years or during years when precipitation arrived during another season.

Measurements of perennial plant diversity are poor predictors of productivity. Those habitats with the highest perennial alpha diversity may be the poorest in terms of plant productivity. The bench, characterized by high perennial diversity, was low in annual diversity and productivity during 1979. On the other hand, the Pueblo Bonito study area was characterized by low perennial plant diversity, but annual plant species were diverse and productivity was high during the favorable year of 1979. Our study indicates that during favorable years, annual plant species have patterns of dominance and diversity that are separate from those of perennial species. Both perennial and annual components should be considered in measurements of diversity and productivity within plant communities.

Acknowledgments

The Division of Cultural Research, National Park Service, Santa Fe, New Mexico, provided funding for the fieldwork portion of this project. Glen Lanier helped gather the annual plant productivity information during 1979. Mollie Toll and Karen Clary helped during 1980 and 1981. Jerry Livingston of the Division of Cultural Research, National Park Service, provided the illustrations.

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ASSOCIATIONS OF SMALL MAMMALS OCCURRING IN A PLUVIAL LAKE BASIN, RUBY LAKE, NEVADA

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ABSTRACT.—Ruby Lake is a highly mesic and vegetationally diverse pluvial lake basin of east central Nevada. Small mammal associations were examined in six plant communities at Ruby Lake using transects of live traps. Small mammal activity was recorded for these six habitats plus an additional three other specialized habitats. A total of 11 species of small mammals were trapped from the six habitat types; from the entire study area 26 species were trapped or observed. Two greasewood shrub habitats and a shadscale–spiny hopsage habitat held the highest number of trapped species, 6, 5, and 7, respectively. The mesic haymeadow and spring habitats, as well as the big sagebrush–antelope bitterbrush habitat held 4 trapped species each. *Peromyscus maniculatus* and *Perognathus parvus* made up 76% of the total captures and were found in all habitat types except marshlands. *Eutamius minimus* was found in four of the six habitat types, while *Dipodomys ordii*, *Dipodomys microps*, *Perognathus parvus*, and *Microtus montanus* were limited to specialized habitats. Mesic adapted, wetland species such as *Mustela vison*, *Ondatra zibethicus*, and *Sorex vagrans* possibly dispersed into Ruby Valley from the northeastern drainages and valleys during the late Pleistocene or Holocene.

Analyses of small mammal communities in the Great Basin have added much to our knowledge of their ecology and biogeographical distributions (Hall 1946, Borrell and Ellis 1934, O'Farrell 1974). The majority of these studies have been concentrated in the more mesic, isolated mountain ranges in plant communities above 2,100 m (Brown 1978). Such research has shown that apparent relictal populations occur isolated on various mountain ranges, analogous to populations on oceanic islands, with little chance of restoring such gene pools by immigration (Brown 1978).

It has been only in recent years that the shrub steppe desert of the valley floors and pluvial lake basins has received attention. Only minor differences in species composition and abundances of small mammals have been shown to occur between the eastern and western halves of the Great Basin. The western and southern deserts are characterized by a transitional zone of desert shrubs such as *Artemisia*, *Sarcobatus*, *Atriplex*, *Larrea*, and *Chenopodium*. The small mammal communities of the Mojave and southern Great Basin deserts are dominated by such heteromyids as *Dipodomys merriami*, *D. microps*, *Perognathus longimembris*, and *P. formosus*. As one moves north and east, the plant communities lose their Mojave Desert affinities, and the small mammal composition of lower elevation communities is dominated by two species, *Peromyscus maniculatus* and *Perognathus parvus* (Durrant 1953, O'Farrell and Clark 1986, Jorgensen and Hayward 1965).

The 53 defined pluvial lake basins of central and eastern Nevada provide an environment for several plant communities that have been progressively adapting to a drier, cooler climate and more alkaline soils since the end of the Pleistocene (Mifflin and Wheat 1976). Lying within the rain shadow of the Sierra Nevada and in the rain shadow of an adjacent mountain range, the pluvial basins today are characterized by low atmospheric precipitation, no external runoff, and limited inflow from a yearly snowmelt that varies from year to year (Mifflin and Wheat 1976). Evaporation of once extensive lake waters left behind high concentrations of saline deposits and thus exposed new habitat and soils for the rapidly evolving phraeophytic shrubs of the genera *Sarcobatus* and *Atriplex* (Young et al. 1986).

While several studies have described the small mammal communities of valley floors dominated by *Artemisia tridentata* (O'Farrell 1974), few have concentrated on the phraeophytic plant communities around pluvial lake basins (Jorgensen and Hayward 1965, Young and Evans 1974). Durrant (1952) and Hall (1946) list several species collected from various localities representing pluvial lake basins in the Great Basin.

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Our purpose here is to describe associations among small mammals within six plant communities surrounding the perennial Lake Ruby, the southern remnant of pluvial Lake Franklin, in northeastern Nevada. We will also compare these small mammal associations with small mammal communities existing in other pluvial lake basins within the Great Basin and possible routes of late Pleistocene or Holocene dispersal.

METHODS AND STUDY AREA

This study was conducted in Ruby Valley, southern Elko County, on the southeastern flank of the Ruby Mountains, Nevada, latitude 40°07′30″ and longitude 115°30′00″. During the late Pleistocene, Ruby Valley, approximately 3,662 sq km, held a large pluvial lake covering some 628 sq km and had estimated depths of 60 m (Mifflin and Wheat 1979). Climatic changes over the last 500,000 years caused this large body of water to recede to its present-day level at an elevation of 1,860 m, resulting in a large seasonal lake and playa near the center of the valley. Today this remnant is called Franklin Lake (USFWS 1987). The northern half of the valley probably had some inflow of water from pluvial Clover Lake to the northeast (Mifflin and Wheat 1979). Today this end of the valley consists of big sagebrush and rabbitbrush (*Chrysothamnus* spp.) uplands, and lower-elevation hay meadows and greasewood (*Sarcobatus* sp.) shrublands.

The southern end of the valley is under the jurisdiction of the Fish and Wildlife Service, U.S. Department of the Interior. In this locality over 200 perennial carbonic rock springs, coming from the eastern flank of the Ruby Mountains, provide a relatively constant source of water for the 15,053-ha Ruby Lake National Wildlife Refuge (USFWS 1987). The perennial springs provide a water source that sustains some unique and diversified plant communities that are very mesic when compared to other pluvial lakes of the region (Mifflin and Wheat 1979).

Delineation of six habitat types was determined by the dominant plant species and comparison with plant communities described for other pluvial lake basins in Nevada (Young et al. 1986). Of the 15,053 ha of refuge, approximately 32% consists of a series of managed wetlands, dikes, and collection ditches used for both fishing and waterfowl production (USFWS 1987). This habitat was not quantitatively sampled due to its aquatic nature; however, observations of mammal use and mammal sign were recorded. All plant names were based on Cronquist et al. (1977) and Johnson et al. (1981). The following habitat types were all sampled for small mammals using quantitative techniques.

HABITAT 1.—A mixed plant community of black greasewood (*Sarcobatus vermiculatus*), big sagebrush (*Artemisia tridentata*), and rubber rabbitbrush (*Chrysothamnus nauseosus*) occupies approximately 10% of the refuge in a belt extending from the southern tip, proceeding north on the east side of the refuge, and terminating near the north end. The understory plants of this habitat are sparse but diverse, including Sandberg's bluegrass (*Poa sandbergii*) and long-leaved phlox (*Phlox longifolia*). A subunit of this habitat included a series of stabilized sand dunes with black greasewood clones on the top of the dune and big sagebrush around the perimeter. Other plants characteristic of the dunes include Indian ricegrass (*Oryzopsis hymenoides*), needle and thread grass (*Stipa comata*), and Hooker's evening primrose (*Oenothera hookeri*). The stabilized dunes make up only 1% of the refuge area, while on other pluvial lake basins in Nevada they are a much more prominent land form (Young et al. 1986).

HABITAT 2.—As one moves closer to the center of the lake from Habitat 1, the soils become noticeably more alkaline and the plant community changes. The dominant shrubs here include black greasewood, shadscale (*Atriplex confertifolia*), alkali rabbitbrush (*Chrysothamnus albidus*), and rubber rabbitbrush. Understory plants are dense but low in diversity. These include salt grass (*Distichlis spicata*), Great Basin wildrye (*Elymus cinerus*), alkali bulrush (*Scirpus paludosus*), and western seepweed (*Suaeda occidentalis*), all of which are salt-tolerant species (Young et al. 1986).

HABITAT 3.—Due to the concentration of springs on the west side of the refuge, the majority of the mesic hay meadows and seasonally wet wire rush meadows are found directly below the slopes of the Ruby Mountains. This habitat is extremely dense and varies in height from 10 cm to 1 m. The dominant vegetation in these meadows consists of Baltic wirerush (*Juncus balticus*), sedges (*Carex* spp.), bulrushes (*Scirpus* spp.), and grasses of the genera *Festuca*, *Hordeum*, and *Agrostis*. Seasonal grazing and mowing for hay is done in these habitats after waterfowl nesting season is over in July (USFWS 1987). This habitat makes up 10% of the total refuge area.

HABITAT 4.—The 200 springs and their drainages make up only 4% of the refuge area but are an extremely important habitat for many mammals. Not only is there a dense growth of *Juncus* and *Scirpus* in such areas but also many mesic shrubs, such as Scouler's willow (*Salix scoueriana*), Wood's rose (*Rosa woodsii*), and golden currant (*Ribes aureum*). The forb and grass species around these springs are very diverse and are usually part of an ecotone area bordered by big sagebrush or hay meadows.

HABITAT 5.—Alluvial fans coming from the eastern slopes of the Ruby Mountains at elevations between 1,800 and 2,100 m constitute 22% of the refuge. The co-dominant shrubs of the community include big sagebrush, antelope bitterbrush (*Purshia tridentata*), western serviceberry (*Amelanchier alnifolia*), and green rabbitbrush (*Chrysothamnus viscidiflorus*). The introduced cheatgrass *Bromus tectorium*, found in many of the high-valley shrub communities, is the dominant grass along with such bunchgrasses as bottlebrush squirreltail (*Sitanion hystrix*) and Indian ricegrass. A very diverse forb component is found here with such dominants as long-leaved phlox, *Aster* spp., scarlet gilia (*Ipomopsis* spp.), and western yarrow (*Achillea millefolium*). This plant community is found primarily on the west side of the refuge as well as the northern and southern ends.

HABITAT 6.—This plant community is characterized by low-growing shrubs with much bare, gravelly ground. It is confined to the eastern side of the refuge situated on the broad alluvial fans coming from the Maverick Springs hills. It is just above Habitat 1 in elevation on the eastern side and makes up 16% of the refuge area. A very dry area, this habitat is dominated by shadscale, spiny hopsage (*Grayia spinescans*), and dwarf sagebrush (*Artemisia arbuscula*). Grasses and forbs are scarce in this area, those seen most often including bottlebrush squirreltail and peppergrass (*Lepidium lasiocarpum*).

This study was conducted during the periods of June–September 1986 and April–October 1987. Its major goal was a general inventory of all small mammals inhabiting the principal habitat types on the refuge. This information was used in the compilation of a wildlife checklist (USFWS 1987).

Several data-collecting techniques were used and all possible habitat types were inventoried in compiling this general inventory. For the previously described six habitat types, a total of 100 Sherman live traps were used for a total of 2,050 trap nights. In each habitat the live traps were placed in two parallel transects of 50 stations each. Single traps were placed 15 paces apart and baited with rolled oats. Each habitat type was trapped at least three consecutive nights. Also used on selected habitats were 15 Tomahawk live traps for squirrels and rabbits and 40 pitfall traps for shrews. Mist nets were utilized on five separate occasions to capture, identify, and release species of bats. All observations of mammals seen or signs of mammals, tracks, and scats were recorded as to species and habitat.

For each animal captured on the trap lines, the sex, age, and reproductive condition were recorded. The majority of the animals were released after identification. Those that died in the traps were preserved and are now housed in the museum of NNCC. Data collected here were analyzed by species, number of captures for each species, and number of captures per 100 trap nights. The relative frequency was calculated for each species in each of the six habitats, and the total number of species captured or observed was tabulated according to habitat. Relative frequency is the number of individuals captured per species divided by the total individual captures of all species, multiplied by 100.

RESULTS

A total of 11 species of small mammals were sampled from the six habitat types in which trap lines were used. The composition of small mammal communities and the relative frequency of each species differed among habitat types (Table 1).

TABLE 1. Small mammals trapped along transects from six habitat types on the Ruby Lake National Wildlife Refuge. C = total captures during period June–September 1986 and April–October 1987. C/T = captures per 100 trap nights. RF = relative frequencies of captures within each habitat type.

	Habitat 1			Habitat 2			Habitat 3			Habitat 4			Habitat 5			Habitat 6		
	C	C/T	RF%	C	C/T	RF%	C	C/T	RF%	C	C/T	RF%	C	C/T	RF%	C	C/T	RF%
Peromyscus maniculatus	75	23	67	98	46	86	29	6	37	48	16	84	60	11	32	1	0.6	1
Eutamius minimus	7	2.2	6	6	2.8	5							14	2.5	7	1	0.6	1
Dipodomys ordii	19	6	17										5	1.0	2	1	0.6	1
Dipodomys microps	8	2.5	7													28	19	33
Microdipodops megacephalus	2	0.6	2															
Perognathus parvus	1	0.3	1	8	3.8	6	1	0.2	1	3	1	5	110	20	59	49	33	57
Perognathus longimembris																5	3.3	6
Reithrodontomys megalotis				2	1.0	2												
Microtus montanus							36	7.4	46	5	1.7	9						
Sorex vagrans				1	0.5	1	12	2.5	16	1	0.3	2						
Onychomys leucogaster																1	0.6	1
Totals	112	34.6		114	54.3		78	16.1		57	19		186	33.5		86	57.1	
Number of species		6			5			4			4			4			7	

Peromyscus maniculatus and *Perognathus parvus* made up 76% of the total captures within the six habitat types. These two species occurred in all six habitat types, with *P. maniculatus* being most common in Habitat 1 (greasewood and big sagebrush); the smallest number of captures was in Habitat 6 (shadscale and spiny hopsage). *Perognathus parvus* occurred in the largest numbers and in approximately equal frequencies in Habitat 5 (big sagebrush and antelope bitterbrush) and Habitat 6 (shadscale, spiny hopsage, and dwarf sagebrush), while in all other habitats this species was represented in very small numbers (Table 1).

Other habitats that contained species in relatively large numbers were specialized habitats tending toward mesic conditions (*Microtus montanus* and *Sorex vagrans* in Habitat 3), sand dunes and sandy soils (*Dipodomys ordii* in Habitat 1), and dry habitats with low-statured shrubs (*Dipodomys microps* in Habitat 6) (Table 1).

Our data, based on species composition among the six habitat types, indicate that Habitats 3 (hay meadows) and 4 (springs) were identical in the species of small mammals present. In addition, both had the lowest number of captures of all the habitat types (Table 1). The greasewood–big sagebrush habitat (1) and the big sagebrush–antelope bitterbrush habitat (5) were also similar because of the presence of species that find both greasewood and big sagebrush suitable habitats. Habitat 1 is enriched with the addition of two heteromyids, *Dipodomys microps* and *Microdipodops megacephalus*, not present in Habitat 5 (Table 1).

The remaining habitats, 6 and 2, were dissimilar in species composition with those described above. Habitat 6 had the highest number of species (seven) with two, *P. parvus* and *D. microps*, making up 90% of the total captures. Habitat 2 (greasewood and grass), although similar in vegetational structure to Habitat 1, lacked three of the heteromyid species and contained two specialized species, *Reithrodontomys megalotis* and *Sorex vagrans*. *Dipodomys ordii* did occur on the periphery of this habitat in a specialized habitat of sandy soils and rubber rabbitbrush, as suggested by kangaroo rat tracks found on the road each day. None were captured on the transect, however.

Besides *P. maniculatus* and *P. parvus*, three other species of mammals proved to be almost as ubiquitous on the refuge. *Eutamius minimus* was most common in the big sagebrush–antelope bitterbrush habitat but was also present in Habitats 1, 2, and 6. *Dipodomys ordii* preferred any habitat containing sandy soils, which included the sand dunes of Habitat 1 and the roadsides of Habitats 5 and 6. Finally, *Sorex vagrans*, an inhabitant of mesic hay meadows (Habitat 3) and springs (Habitat 4), also occurred in the much drier habitat of greasewood and grass (Habitat 2) (Table 1).

TABLE 2. Small mammals trapped or observed on the Ruby Lake National Wildlife Refuge and associated plant communities, 1986–1987.

	Habitat						Marsh-	Cliff	Home-
Species	1	2	3	4	5	6	lands	sites	steads
Sorex vagrans		x	x	x					
Myotis evotis								x	x
Myotis leibii								x	x
Mustela frenata			x	x					
Mustela vison				x			x		
Taxidea taxus	x				x			x	
Lepus californicus	x	x			x				
Sylvilagus nuttelli				x	x			x	x
Sylvilagus idahoensis	x				x				
Eutamius minimus	x	x			x	x		x	x
Spermophilus lateralis								x	x
Spermophilus townsendii				x	x				
Spermophilus beldingi				x	x				
Thymomys talpoides		x	x	x		x			
Dipodomys ordii	x				x	x			
Dipodomys microps	x					x			
Microdipodops megacephalus	x								
Perognathus parvus	x	x	x	x	x	x		x	
Perognathus longimembris						x			
Peromyscus maniculatus	x	x	x	x	x	x		x	x
Reithrodontomys megalotis		x							
Onychomys leucogaster						x			
Neotoma cinereus								x	x
Microtus montanus			x	x			x		
Ondatra zibethicus							x		
Total species	9	7	6	10	10	8	3	9	7

Although information on sex, reproductive status, and age by pelage was recorded for most individual captures, only data for *P. maniculatus* and *P. parvus* proved significant enough for comparison within Habitats 1, 2, and 5.

Table 2 shows the occurrence of all 25 mammal species trapped or observed during the study period. Included are the six habitat types used in Table 1 as well as three others where trap lines were not used. These three habitats include the large cattail (*Typha* sp.) and bulrush (*Scirpus* sp.) marsh, cliff sites and carbonaceous rock caves around the periphery of the refuge, and homestead that includes the refuge headquarters and Gallegher Fish Hatchery (USFWS 1987). Two common species of bats in the area include a bachelor roost of *Myotis evotis* and *Myotis leibii* from the Cave Creek grotto and a series of lactating females from the Maverick Springs area. Small carnivores captured or observed are listed according to habitat (Table 2). These include *Mustela frenata*, *Mustela vison*, *Canis latrans*, and *Taxidea taxus*. Ground squirrel species were limited to colonies and to a short season of activity in both years. These species include *Spermophilus townsendii*, *S. beldingii*, and *S. lateralis*. Leporids included *Lepus californicus*, *Sylvilagus nutellii*, and *S. idahoensis* (Table 2). The pygmy rabbit was closely associated with stands of big sagebrush around the periphery of the sand dunes in Habitat 1, while Nuttell's cottontail occurred in dense cover along sagebrush roadsides, cliff sites, and homesteads. Large rodents that can be considered habitat specialists include *Ondatra zibethica* in the marsh lands, *Neotoma cinerea* in cliff sites and homesteads, and *Thomomys talpoides* in Habitats 2, 3, and 4 (Table 2).

DISCUSSION

Ruby Lake has been shown to have a large number of diverse plant communities and to be one of the most perennial and mesic of the pluvial lake basins still existing in Nevada today (USFWS 1987). Mifflin and Wheat (1979) suggest that the flora and hydrologic makeup of Ruby Lake as seen today may be reminiscent of what the drier pluvial lakes of west central Nevada looked like during the more mesic late Pleistocene era. This may account for the similarities in small mammal communities seen at Ruby Lake, as compared to the Carson Sink basin in western Nevada (Hall 1946) and the Mono Lake basin of California (Harris 1982).

Both of these pluvial lakes are much drier and contain more seasonal, ephemeral wetlands. The only major difference between these pluvial lakes and the western Great Basin desert in general (Kenagy 1973, Jorgensen and Hayward 1965) is that the small mammal communities are dominated by four to five species of heteromyid rodents, whereas the more eastern pluvial lake mammal communities are dominated by only two species, *P. maniculatus* and *P. parvus*, both adapted to a wide range of habitats but less frequent in hot desert environments (O'Farrell 1974).

River valleys and Pleistocene lake connections allowed easy dispersal routes for wetland- and shrubland-adapted mammals (Hall 1946). This would account for the many similarities in species composition between pluvial lake basins in the Great Basin. While we recorded 24 species of small mammals at Ruby Lake, Young and Evans (1980) list 22 species for pluvial Lake Gilbert in Grass Valley of central Nevada, Hall (1946, 1981) lists 24 species for the Carson Sink desert of western Nevada, and Harris (1982) lists 26 species for the lower elevation habitats of the Mono Lake basin. All of these basins contain a majority of the same species, with only a few differences due primarily to the influx of Mojave Desert fauna into the western Great Basin (Jorgensen and Hayward 1965).

Few studies have been done which permit a quantitative comparison of small mammal communities in pluvial lake basins. O'Farrell (1986) studied five habitat types in Whirlwind Valley, a nonpluvial basin, 120 km NW of Ruby Lake. Here O'Farrell trapped 11 species of small mammals, compared with 14 species in Grass Valley (Evans and Young 1986), and 11 species for Ruby Lake (Table 1). Species composition between these three localities varied only slightly; *P. maniculatus* and *P. parvus* made up the majority of the individuals for each locality in all habitats sampled. Kenagy (1973) and Harris (1982) found that heteromyid rodents were the dominant species in the western deserts and at Mono Lake, but *P. maniculatus* and *P. parvus* were present and widespread. The contribution and relative frequency of each species varied among habitat types at Ruby Lake. We found that the greasewood–big sagebrush habitat had the largest number of species present during the study period. This was also the case in Grass Valley (Evans and Young et al. 1986) and in Whirlwind Valley (O'Farrell 1986). Rodent species diversity has been correlated with resource abundance (Whitford 1976) and with vegetation structure and diversity of a habitat (Rosenzweig and Winakur 1969). Our data agree with these studies in reference to the complexity and relative abundance of forbs and grasses in the greasewood–big sagebrush habitat.

Data recorded for the reproductive activity of *P. maniculatus* in the greasewood–big sagebrush habitat show that the sex ratios did not differ significantly from a 1:1 ratio. Pregnant females and scrotal males, some in juvenile pelage, were common in both May and mid-August, suggesting at least two litters for this habitat during the two years. This would indirectly suggest a habitat rich in resources.

The big sagebrush–antelope bitterbrush habitat has been attributed with a community complexity and richness capable of supporting a small mammal community of 7 (Lent and Eckert 1982) to 12 (O'Farrell 1974) species. At Ruby Lake we captured only 4 species of small mammals in a habitat that seemed to be structurally diverse and rich in forbs and grasses. One possible explanation for the low diversity in this habitat could be the comparatively low number of trap nights. Another possibility is that the high frequency of *P. parvus* (59%) may limit the numbers of other rodent species, such as *Onychomys leucogaster* and *Lagurus curtatus*, which have been captured from this locality and habitat by Borrell and Ellis (1934). Also *P. parvus* has been shown to have an intricate relationship with the antelope bitterbrush in collecting and caching its seeds (Evans et al. 1982). From our data we found that sex ratios for *P. parvus* did not differ significantly from a 1:1 ratio. The greatest reproductive activity occurred in mid-June, and the largest number of juveniles appeared in August. This suggests only one litter for each of the two seasons we sampled in this habitat and agrees with the findings of O'Farrell et al. (1974) in a similar habitat.

The shadscale-spiny hopsage habitat was unusual in that its low stature and low plant complexity nonetheless maintained a high species diversity of seven species. O'Farrell (1986) found that species composition of any one of the five habitats in Whirlwind Valley experienced seasonal changes in species composition. We suspect that this is also the case with the shadscale habitat at Ruby Lake, which was trapped only twice during the late summer. Four of the seven species in this habitat were probably wandering from adjacent greasewood habitats. Two dominant species within this habitat, *P. parvus* and *D. microps*, were also found to be co-dominants at Grass Valley (Young et al. 1980) and Whirlwind Valley (O'Farrell 1986) in a similar shadscale community. *Perognathus longimembris* was found only in the shadscale habitat at Ruby Lake. It did not occur in Whirlwind Valley (O'Farrell 1986) but was found in greasewood habitat in Grass Valley (Young et al. 1980). We found four of the five captured individuals to have interesting patterns of pure white spots on the dorsum, the backs of the ears, and the anterior flanks. These spots are white down to the integument and vary from a coverage of 1/3 of the pelage to minute spots. This pelage has been recorded elsewhere in specimens of *P. longimembris* from the desert of Millard County, Utah (Durrant 1952). *Dipodomys microps* has been shown to have a dietary reliance on the leaves of *Atriplex* rather than on seeds. This accounts for the large numbers of this heteromyid in the shadscale habitat (Kenagy 1973).

Other small mammal associations on Ruby Lake suggest habitat expansions and historical changes in status of some species. At Ruby Lake we found *Eutamius minimus* in four of the six habitat types, being most common in the big sagebrush–bitterbrush habitat. O'Farrell (1986) found the least chipmunk restricted to a greasewood habitat by the presence of the antelope ground squirrel (*Ammospermophilus leucurus*), which occurred in three habitat types. At Grass Valley the least chipmunk was found both in greasewood and in sagebrush but not in all sagebrush habitats or in shadscale because of the presence of the antelope ground squirrel. Robey et al. (1986) showed the least chipmunk to occupy a narrow niche breadth in a desert shrub community shared with the antelope ground squirrel, a species occupying a wide niche. These observations suggest that the least chipmunk at Ruby Lake has expanded into all available shrub habitats in the absence of competition with the antelope ground squirrel, a species not known from Ruby Valley. Brown (1978) describes another instance of habitat expansion in three species of montane chipmunks whose irregular distributions on mountain ranges in eastern Nevada result in atypical habitat utilization by these species and expansion into habitats they normally do not occupy.

Borrell and Ellis (1934) trapped and collected data on mammals from the western flank of the Ruby Mountains along the west edge of Ruby Lake. They found both the mink (*Mustela vison*) and the muskrat (*Ondatra zibethicus*) present in 1927, years before the lake came under government management. This suggests that both are native and possibly dispersed south from the Columbia basin into Mary's River and the wetlands of Pleistocene Clover Lake. This wetland possibly had a Pleistocene connection with pluvial Franklin Lake and Ruby Lake (Mifflin and Wheat 1979).

The same route of dispersal could be applied to the vagrant shrew and the montane vole, both of which occur in the Mary's River basin, the Humboldt River basin, the South Fork and North Fork of the Humboldt River, and the western flank of the Ruby Mountains, all below 1,590 m in elevation (Ports, unpublished data). The presence of *Sorex preblei*, a rare shrew of shrublands and wetlands, in the vicinity of the Great Salt Lake (Tomasi and Hoffmann 1984) and in the Mary's River basin (Ports, unpublished data) suggests the possible occurrence of this species in Clover Valley as well as Ruby Valley.

The pluvial lake basins of the Great Basin provide many mosaic and diverse plant communities for the development of small mammal communities. Similar in species composition and plant communities, these basins have undergone similar climatic changes and have provided easy dispersal routes for populations of wetland- and desert-adapted mammals. Unlike their contemporaries on nearby isolated mountain ranges in subalpine and alpine habitats, the lower-elevation populations of small mammals can be expected to experience a wide range of population mixing and a wider range of dispersal than previously supposed, as seen in the vagrant shrew (Ports, unpublished data). However, we must consider not only the effects of long-term climatic changes on these populations but also their effects on species composition. Studies of greater detail and of longer duration are necessary to understand the influence man has made on the pluvial basin plant and animal communities of the Great Basin.

ACKNOWLEDGMENTS

We wish to thank our sons, Roger and Mark, for their enthusiastic service in the field, as well as Sara Brown of the Ruby Lake Wildlife Refuge for her generous cooperation and suggestions. Charles and Elaine Knight provided us with more than ample facilities while in the field, for which we are grateful.

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UTAH CHUB (*GILA ATRARIA*) FROM THE LATEST PLEISTOCENE GILBERT SHORELINE, WEST OF CORRINE, UTAH

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ABSTRACT.—A bulk sampling of gastropods collected near Great Salt Lake, Utah, revealed several fish bones of *Gila atraria* (Girard). The early date of this find, coupled with the relationship of the Gilbert lake transgression and successive regression of approximately 11,000 years B.P., reveals a death assemblage induced by a series of saline inundations into the freshwater paludal environment.

A large death assemblage of late Pleistocene gastropods, lying in an exposed roadcut along State Highway 83, 17.5 km northwest of Corrine, Utah (UTM coordinates 0390500E/4606400N, Public Shooting Grounds, 7.5 minute quadrangle), was radiocarbon dated by Miller (1980), twice by Currey (1988), and by the author. The respective dates of 10,920 ± 150 C-14 years B.P. (W-4395), 11,990 ± 100 C-14 years B.P. (Beta-16912, 11,570 ± 100 C-14 years B.P (Beta-16913), and 10,990 ± 110 C-14 years B.P. (Beta-22431) imply a period of low lake level before the Gilbert rise of 11,000 years B.P. (Currey and Oviatt 1985). Currey (1980), Miller et al. (1980), Scott et al. (1983), and Currey and Oviatt (1985) use data from this site to assign the Pleistocene-Holocene boundary to Great Salt Lake and its predecessor. The discovery of *Gila atraria* at this site provides a unique opportunity for understanding late Pleistocene and early Holocene environmental conditions and lake level fluctuations.

Gastropods from the Public Shooting Grounds were collected in 1987 for further identification of representative genera, species, and habitat. The gastropod genera *Amnicola, Helisoma, Lymnaea*, and *Physella* (Table 1) were excavated from a sand unit overlain by an organic marsh deposit. The fossil gastropods and *Gila atraria* were sampled at an altitude of 4,232 feet (1,290 m) a.s.l. Laboratory cleaning of the shells consisted of ultrasonic washing in deionized water and air drying. Several unexpected rib, pharyangeal, vertebral, and maxillary bones of *Gila atraria* (Utah chub) were discovered within the matrix of this gastropod-rich sand unit. The bones were identified in 1987 by Mark Rosenfeld of the Department of Biology at the University of Utah.

Today's Utah chub are native to Utah, a small part of Nevada, and Idaho and are common in several rivers draining into Great Salt Lake (Rawley 1980) in the Bonneville basin. Stokes et al. (1964) and Smith et al. (1968) report gastropod species and *Gila atraria*, with respective dates of 13,000 years B.P. (estimate) and 12,860 ± 100 years B.P. (W-2000), from two sites above 4,440 feet (1,350 m) on the margins of a regressive Lake Bonneville. This euryphagic species inhabits pelagic and littoral epilimnion areas (Varley and Livesay 1976).

STRATIGRAPHY

The oldest exposed sediments from the Public Shooting Grounds site are the post-Provo to pre-Gilbert red beds (calcareous muds and minor sands). The red beds were reddened off-site and deposited basinward on mudflats and sandflats of the newly exposed regressive Bonneville basin about 13,000 years B.P. (Currey et al. 1988). The red bed deposition continued for about 1,000 years due to sediment washing into lower basin areas. This regressive stage led to the precipitation of Glauber's salt ($Na_2SO_4 . 10 H_2O$) at the deepest portion of the present Great Salt Lake (Currey and Oviatt 1985). A transgressive episode of green, muddy sands, which have a minimum limiting date of 12,000 years B.P.

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TABLE 1. Gastropod species and total percentage concentration. Sources: Chamberlin and Jones (1929) and fieldwork (1987–88).

Species	Habitat	Concentrations (%)
Helisoma trivolvis	Quiet to stagnant fresh water	5
Physella utahensis	Ponds and streams	7
Lymnaea stagnalis	Ponds, lakes, and streams often attached to plants	8
Amnicola limosa	Streams, rivers, and more quiet bottom waters	80

(Beta-16912-3, Currey et al. 1988), unconformably overlies the red beds and grades upward into the Gilbert shoreline deltaic sediments. Currey (1980), Scott et al. (1983), and Currey and Oviatt (1985) suggest that the Gilbert shoreline represents a fluctuating stand followed by a regressive interval to lower lake stages. The green, muddy sand exposure is common to ancient lake basins and represents a reducing environment with a high ferric iron content (Reeves 1968). Successive layers of fine, clean, silty sands and marshy deposits of the Bear River and possibly the Malad River lie conformably over the green, muddy sands. The first layer consists of clean, fine sands and is interpreted as a 10- to 20-foot (3- to 6-m) minor transgression. As the lake regressed, a dark organic layer, indicating high humic concentrations, appears predating the death assemblage. This organic layer is overlain by lacustrine silts and represents the second transgressive saline inundation of the fluctuating Gilbert stand. Three additional episodes of saline, fossil-rich sediments and subsequent clean, fine sand deposits are recorded in this banded exposure. During the third minor regression, four genera of gastropods and *Gila atraria* migrated basinward previous to 10,990 ± 110 C-14 years B.P. (Beta- 22431), a date that is based on a species-specific sample of *Lymnaea stagnalis* shells.

Gastropods are typically found in freshwater streams and ponds and usually feed on aquatic plants and organic detritus (Chamberlin and Jones 1929). *Gila atraria*, at the Public Shooting Grounds site, would have taken advantage of this newly formed marsh habitat that existed after previous saline water inundations. These faunas are suspended in a death assemblage matrix of trangressive lacustrine sands and silts. The beginning of the next transgression probably killed the remainder of freshwater organisms in this paludal margin, laying down the final, thick shell layer containing *Gila atraria*. This final, highest fossiliferous layer is 7.5 inches (19 cm) thick and is overlain by light brown, fine sands. Two organic marsh layers of 1.75 to 3 inches (4.4 to 7.6 cm) overlie the death assemblage. These undated layers are thought to be the last marsh deposits prior to the transgression that geomorphically marks the highest stage of the Gilbert shoreline. A fine, poorly sorted, nearshore sand layer deposited by this Gilbert high stage and a 4- to 5-inch (10- to 12.7-cm) modern soil comprise this exposure (Fig. 1).

DISCUSSION

The paleoenvironment of *Gila atraria* was probably an ephemeral, shallow, freshwater marsh that is evident today at lower elevations in the area. Aquatic plants, pioneering organisms, insects, and detritus would have provided a minimum of sustenance for the euryphagic *Gila atraria* and gastropod species.

As the lake transgressed, gastropods died and were deposited in 3- to 7.5-in (7.6- to 19-cm) layers within weak sand matrices. It is inferred from the thickness of these layers that the paludal margins were inundated by saline water depositing the faunal remains in small depressions. Due to the quality of the remains, it is hypothesized that the fossils were covered by nearshore sands rather quickly.

Pleistocene-Holocene transitions in Great Salt Lake marginal deposits tend to have had faunal assemblages that are restricted to gastropods. The discovery of *Gila ataria* in these deposits, with radiocarbon date association, suggests greater faunal diversity than previously thought.

ACKNOWLEDGMENTS

Support facilities were provided by the Vasyl Gvosdetsky Laboratory for Environmental and Paleoenvironmental Studies and the Quaternary Research fund of the Department of Geography at the University of Utah.

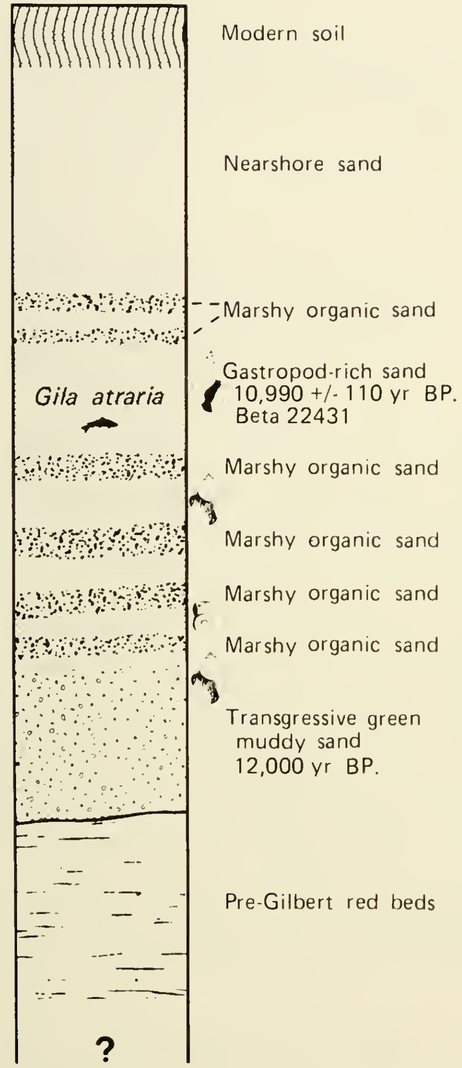

Fig. 1. Generalized stratigraphic column containing *Gila atraria*; radiocarbon date on *Lymnaea s.*

I acknowledge Dr. Jeanne Kay and Dr. Donald Currey for their valuable comments and improvements on this manuscript.

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MEDIATION OF NUTRIENT CYCLING BY ARTHROPODS IN UNMANAGED AND INTENSIVELY MANAGED MOUNTAIN BRUSH HABITATS

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ABSTRACT.—The role of arthropods in mediating nutrient cycling on a community level was examined in a mountain shrub habitat that was managed by mowing brush to a 20-cm stubble, applying aerially 2,4-D butyl ester, or burning sixteen 4-ha study sites. Malathion and carbaryl were used to decrease arthropod populations. Higher nutrient concentrations occurred in the litter and foliage than in the soil of unmanaged habitats. Arthropods decreased nutrient concentrations in litter and foliage in unmanaged and herbicide-sprayed sites. Arthropod populations increased nutrient concentrations in mowed and burned sites. Nitrogen was consistently affected by both arthropods and brush management in all habitats.

Regulation of nutrient cycling by arthropods appears to be a function of the frequency and severity of habitat disturbance (Schowalter 1986). Arthropod responses to perturbances appear to stabilize ecosystem productivity through regulating plant, soil, nutrient, and light relations by changing plant structure and plant species biomass (Mattson and Addy 1975). In addition, the severity of a disturbance may be reduced by increasing its reliability. Plant age structure as well as plant biomass is changed as old, nonproductive plants and plant parts are eaten or reduced to litter by arthropods. This process also has an effect on nutrient release and containment in a habitat (Schowalter 1986).

Phytophagous insects require proteinaceous nitrogen for their life cycles. When the nitrogen level in plants increases, insect assimilation and growth efficiencies increase (Mattson 1980). Thus, although high nitrogen levels can be detrimental to some insects (Stark 1965), evidence suggests that insects will generally seek and respond to high nitrogen levels (Prestidge and McNeill 1965). Higher available nitrogen levels can be found in annual plants as compared to perennial plants. Being short-lived, annuals do not commit high levels of energy to defensive chemistry but allocate most of their energy to reproduction. Therefore, insect feeding can result in an increase of nutrient and energy flow in annual plants as they recover from nitrogen loss (Grimes 1979). Other inorganic elements, such as calcium, magnesium, phosphorus, potassium, and sodium, are vital to diets of many insects (Dadd 1977, 1985), and these elements are likely regulated to some extent in the environment by insects.

The role of arthropods in forest nutrient cycling has been studied by Cornaby (1977), Crossley (1977), and Webb (1977). However, few studies have been conducted on nutrient cycling in the sagebrush/bitterbrush system. Because of the lack of research in this area, we undertook this study with two objectives in mind. The first was to determine if arthropods were a mediating factor in nutrient cycling, on a community level, in a sagebrush habitat. The second objective was to determine if habitat disturbance would influence the role of arthropods in nutrient cycling.

MATERIALS AND METHODS

This study was conducted on a sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*) habitat located at an elevation of 2,400 m, 12 km southeast of Saratoga, Carbon County, Wyoming. Precipitation averaged 480 mm per year, mostly in the form of snow. Temperatures ranged from 21.0 to 27.0 C during the 100 days of the summer study period though the mean annual temperature is 10.2 C. Soils are the North Park Formation of brown sandy loams developed on loess, limestone, sandstone, and tuff.

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The study site consisted of 16 blocks of at least 4 ha each. These blocks were randomly chosen from sites that had similar vegetation, soil chemistry, and soil texture characteristics. Habitat manipulation in May 1986 consisted of either mowing four 4-ha blocks to a 20-cm stubble height or applying 2,4-D butyl ester in water at an aerial rate of 0.91 kg per hectare to four 4-ha blocks. In the fall of 1986, four 4-ha blocks were burned. These treatments are used as sagebrush management practices in Wyoming. Control blocks consisted of four 4-ha, unmanaged, high-density shrub areas.

Arthropod populations were reduced using two insecticides, carbaryl (1.68 kg/ha) and malathion (1.4 kg/ha). These compounds were alternately applied every two weeks from early May through August of 1987 to half of each block in the managed and unmanaged areas. The other half of each block was left untreated as a control.

To determine effectiveness of insecticide treatments, we estimated arthropod densities using 100 sweeps of a 38-cm diameter sweep net to collect arthropods along three 100-m transects in both closed (covered by brush canopy) and open (not covered by brush canopy) microhabitats in each managed and unmanaged split-plot every 10 days.

Foliage, litter, and soil samples were collected in open and closed microhabitats in early September 1987 from fifteen 0.25-m^2 quadrats located along three 100-m transects in each split-plot. Samples were placed in paper bags, returned to the laboratory, and dried for three days at 75 C. All foliage and litter samples were ground in a Wiley Mill with a 40-mesh screen.

Total nitrogen for litter, plant, and soil material was determined by the use of a block digestion method and analysis (Jones 1971). Concentrations of magnesium, calcium, phosphorus, potassium, and sodium were determined by the Havlin and Soltanpour (1980) method of nitric digestion. All nutrient concentrations except for phosphorus, which was determined by the Olsen and Dean (1960) colorimetric method, were determined by the use of plasma spectrometry. Soil pH, electrical conductivity, and soluble cation analysis were evaluated with methods of Richards (1980). Soil organic matter was determined by combustion (Grewling and Peech 1965). Texture analysis applied the theory of particle fractionation as used by Day (1965).

TABLE 1. Vegetation parameters as determined for the baseline year (1985), treatment year (1986), and recovery year (1987).

Treatment	Year		
	1985	1986	1987
	Herbaceous biomass (g/m^2)[a]		
Unmanaged	7.0a	7.2a	5.7a
Herbicide	7.3a	16.7b	29.1c
Mowed	7.4a	24.0b	23.0b
Burned	7.2a	7.4a	4.3b
	Litter biomass (g/m^2)[a]		
Control	78.0a	79.6a	87.1a
Herbicide	75.8a	77.3a	73.1a
Mowed	79.0a	291.2b	287.6b
Burned	76.4a	77.7a	2.3b
	Sagebrush density (%)[b]		
Control	54.7a	54.8a	55.9a
Herbicide	47.9a	21.8b	18.0b
Mowed	63.7a	32.0b	38.0b
Burned	60.2a	59.7a	5.7b
	Bitterbrush density (%)[b]		
Control	54.0a	55.0a	57.0a
Herbicide	14.4a	45.7b	64.0c
Mowed	41.4a	51.4b	52.0b
Burned	47.4a	48.1a	6.3b
	Total shrub cover (%)[b]		
Control	28.1a	28.1a	29.0a
Herbicide	29.6a	17.5b	17.0b
Mowed	31.6a	24.0b	23.0b
Burned	30.3a	29.8a	6.2b

[a] Means for a parameter within a treatment between years followed by the same letter are not significantly different ($P = .05$; LSD Test [Fisher 1949]). $N = 60$ samples.

[b] Means for a parameter followed by the same letter are not significantly different ($P = .05$; Chi-square). $N = 60$ samples.

The results were analyzed as a split-plot design, and Fisher's (1949) protected least significant difference test was employed to compare specific treatment effects on nutrient content of foliage and litter. Chi-square analysis was used to assess differences in the proportions of shrub cover between management areas. In all statistical tests, differences were considered significant at $P < .05$.

RESULTS AND DISCUSSION

Disturbance of vegetation by brush management practices resulted in significant decreases in density of the major overstory plant species, sagebrush and bitterbrush (Table 1). Herbaceous biomass increased dramatically in both mowed and herbicide-sprayed blocks during and after the year of management, as

TABLE 2. Nutrient concentrations (ppm) of soil, litter, and foliage in sagebrush/bitterbrush habitats before management procedures were applied.

Nutrient[a]	Habitat	Soil	Litter	Foliage[b]
Nitrogen	Closed	21.00a	96.00c	112.00e
	Open	23.50ab	104.00d	149.00f
Potassium	Closed	.48a	2.54cd	10.75e
	Open	.54ab	1.78bc	9.68de
Magnesium	Closed	.70a	1.45d	1.01abc
	Open	.84ab	.84ab	1.90e
Sodium	Closed	.02a	.11d	.04b
	Open	.09c	.02a	.02a
Phosphorus	Closed	.69ab	.54a	1.19c
	Open	.74b	.72b	.92b
Calcium	Closed	4.98ab	8.49d	4.17a
	Open	5.23abc	5.65bc	8.10d

[a] Means for a nutrient followed by the same letter are not significantly different ($P = .05$; LSD Test [Fisher 1949]). $N = 60$ samples.

[b] Closed foliage indicates shrubs and open foliage indicates grass.

often occurs with the decline of the shrub layer (Barbour et al. 1980). Litter biomass significantly increased during and after the year of mowing. Both herbaceous and litter biomass decreased significantly after being burned.

In undisturbed sites the vegetation component contained higher concentrations of nitrogen, potassium, and magnesium than the litter, which had higher concentrations than the soil (Table 2). Phosphorus levels were higher in shrub vegetation than in any other component. This was probably due to long-term accumulation of this element in the woody portion of shrubs, as is known to occur in forest habitats (Horn 1974). Calcium was highest in the litter of closed microhabitats and in grasses. Sodium concentrations were highest in litter located under shrubs. Sodium is readily leached from open litter (Forth and Turk 1972). Thus, sodium concentration under shrubs may have been higher due to more protection from precipitation and leaching.

Insecticide applications reduced arthropod densities by 82% in unmanaged areas, 76% in mowed areas, 74% in herbicide-applied areas, and 78% in burned areas (Table 3). All orders were clearly diminished by the insecticides, although Acari generally fared better than the insect orders.

The nutrient levels in unmanaged habitats with intact arthropod communities compared well with previous measurements in sagebrush (Gough and Erdman 1980). Arthropods in open microhabitats of unmanaged blocks significantly increased nitrogen, magnesium, and calcium in both litter and foliage (Table 4). Phosphorus was significantly decreased in foliage of open microhabitats by arthropods. Foliage potassium significantly increased in insecticide-treated, open areas. Arthropods significantly increased nitrogen in both litter and foliage of closed microhabitats and significantly increased potassium in litter. Arthropods significantly decreased magnesium and sodium in both litter and foliage in closed microhabitats and significantly decreased phosphorus in foliage of closed microhabitats.

Decreases in the level of a nutrient following insecticide applications indicate that arthropods have some direct or indirect effect on the release of these nutrients. In particular, arthropods are clearly acting to increase plant nitrogen, since this element decreased significantly in foliage and litter of open and closed microhabitats after insecticide treatments. There is some evidence that insect feeding may stimulate plant growth (Walmsley et al. 1987), and this effect may account for the impact of arthropods on plant nitrogen levels. Since arthropods function in unmanaged sagebrush habitats to increase the levels of nitrogen in plant material, the indirect impacts of widespread applications of broad-spectrum insecticides on western prairies for control of grasshoppers should be considered (Hewitt and Onsager 1983).

Insects may also be functioning to directly mobilize nutrients; aphids are a good example of how insects may mediate nutrient cycling. As a group, aphids are generally inefficient at energy conversion of plant sap; only 5% of the potential dietary energy is utilized, and the remainder is excreted as honeydew (Hagen et al. 1951). This product is nutritionally important to a number of animals and fungi (Wilson 1971). As such, honeydew production functions as an important and rapid return of energy and nutrients to the local habitat. Soluble nutrients in the phloem are absorbed by aphids and provide food to other organisms through honeydew or indirectly through predation. Therefore, aphids and other arthropods may act as nutrient-storage organisms or sinks for plant nutrients in a small scale (Way and Cammell 1970). Joy (1967) reported that local amino acid synthesis can be induced from nutrients contained in the aphid sink.

The reduction of arthropod population density by insecticides in herbicide-treated sites

TABLE 3. Effects of insecticide treatments on arthropod population densities (no./m^2) in unmanaged, mowed, and herbicide-managed blocks averaged over the study.

		Unmanaged		Mowed		Herbicide	
Order	Habitat	Treated	Control	Treated	Control	Treated	Control
Acari	foliage	0	0	2	0	2	0
Araneae	foliage	6	1	2	0	3	1
Homoptera	foliage	218	41	35	10	39	7
Coleoptera	foliage	6	1	15	1	6	3
Diptera	foliage	16	2	3	0	2	1
Hymenoptera	foliage	62	10	72	29	85	24
Acari	litter	495	95	640	170	677	175
Araneae	litter	9	2	6	0	7	1
Homoptera	litter	11	0	11	2	12	4
Coleoptera	litter	13	0	9	0	10	2
Diptera	litter	24	5	13	1	25	7
Hymenoptera	litter	16	0	12	0	13	0
Collembola	litter	14	3	93	18	63	16
Thysanura	litter	6	1	8	0	3	0
% decrease			82%		76%		74%

TABLE 4. Arthropod effects on nutrients (ppm) in unmanaged sagebrush/bitterbrush habitats treated with insecticides.

		Foliage		Litter	
Nutrient[a]	Habitat	Treated	Untreated	Treated	Untreated
Nitrogen	Closed	100.00cde	112.00f	69.00a	96.00cd
	Open	87.00cb	149.00e	82.00b	104.00ed
Magnesium	Closed	1.29cd	1.01abcd	1.94g	1.45def
	Open	0.92cab	1.90g	0.75a	0.84ab
Calcium	Closed	4.17a	4.17a	8.87ed	8.49d
	Open	4.78ab	8.10d	4.78ab	5.65c
Sodium	Closed	<.01a	0.04abc	0.14e	0.11d
	Open	0.04abc	0.02ab	<.01a	0.02ab
Potassium	Closed	11.51g	10.75g	1.58ab	2.45cd
	Open	8.51f	5.59e	1.00ab	0.54a
Phosphorus	Closed	1.61g	1.19ef	0.56abc	0.54abc
	Open	1.15e	0.92d	0.57abc	0.72abc

[a] Means for a nutrient followed by the same letter are not significantly different (P .05, LSD Test [Fisher 1949]). N 60 samples.

resulted in a significant decrease of all litter nutrients except sodium (Table 5). However, only phosphorus was significantly decreased in foliage. Again, the decrease of nutrients when arthropod populations were reduced in herbicide-treated areas could be the result of arthropods being storage components in the community as in undisturbed sites. The application of herbicide effectively eliminated the closed microhabitat.

In herbicide-treated mountain brush habitats, arthropods functioned to generally increase litter nutrient levels. Whether insects directly (via death and decomposition) or indirectly (via secretions and excretions) elevate litter nutrient levels is yet to be determined. The general lack of change in foliage nutrient levels suggests that the loss of nutrients in litter following insecticide treatments did not result in the effective mobilization of the nutrients for uptake by grasses. Many of the annual grasses may not have been in a phenological stage suitable to exploit the available resources as they became available in mid- to late summer.

Application of insecticides to mowed sites caused significant increases of litter nitrogen, potassium, and phosphorus in open microhabitats (Table 6). The increase in phosphorus could be an artifact from application of the organophosphorous insecticide. Canopy-covered litter in insecticide-treated plots had significant increases in nitrogen, magnesium, and calcium. There were significant decreases of foliage magnesium and phosphorus in

TABLE 5. Arthropod effects on nutrients (ppm) in herbicide-treated sagebrush/bitterbrush habitats treated with insecticides.

		Foliage		Litter	
Nutrient[a]	Habitat	Treated	Untreated	Treated	Untreated
Nitrogen	Open	142.00b	142.00b	55.00a	146.00b
Magnesium	Open	0.91ab	0.86ab	0.91ab	1.03c
Calcium	Open	6.62b	6.30b	4.05a	6.42b
Sodium	Open	<.01a	0.04a	0.32b	<.01a
Potassium	Open	7.12c	7.12c	0.47a	1.12b
Phosphorus	Open	0.98b	1.24c	0.24a	0.94b

[a]Means for a nutrient followed by the same letter are not significantly different (P = .05, LSD Test [Fisher 1949]). N = 60 samples.

TABLE 6. Arthropod effects on nutrients (ppm) in mowed sagebrush/bitterbrush habitats treated with insecticides.

		Foliage		Litter	
Nutrient[a]	Habitat	Treated	Untreated	Treated	Untreated
Nitrogen	Closed	122.00c	120.00c	117.00c	99.00b
	Open	114.00c	139.00d	119.00c	85.00a
Magnesium	Closed	1.13cd	1.48e	1.48e	0.68a
	Open	1.17cd	0.96bcd	0.93bc	0.88ab
Calcium	Closed	4.71a	6.78abcd	9.05g	6.78ef
	Open	5.94abcde	5.12abc	5.07ab	5.63abcd
Sodium	Closed	<.01a	0.03a	<.01a	0.30b
	Open	<.01a	0.03a	<.01a	0.04a
Potassium	Closed	11.13g	10.79g	2.05abcd	0.85ab
	Open	0.74a	6.24ef	5.34e	0.93abc
Phosphorus	Closed	0.98f	1.40g	0.53abc	0.33ab
	Open	0.58cd	0.66de	0.70e	0.32a

[a]Means for a nutrient followed by the same letter are not significantly different (P = .05, LSD Test [Fisher 1949]). N = 60 samples.

TABLE 7. Arthropod effects on nutrients (ppm) in burned sagebrush/bitterbrush habitats treated with insecticides.

		Foliage		Litter	
Nutrient[a]	Habitat	Treated	Untreated	Treated	Untreated
Nitrogen	Open	NA	NA	215.00a	204.00a
Magnesium	Open	NA	NA	3.60a	2.85b
Calcium	Open	NA	NA	8.65a	7.69a
Sodium	Open	NA	NA	0.04a	<.01a
Potassium	Open	NA	NA	43.57a	29.52b
Phosphorus	Open	NA	NA	2.30a	1.83b

[a]Means for a nutrient followed by the same letter are not significantly different (P = .05; LSD Test [Fisher 1949]). N = 60 samples. NA = not applicable.

canopy-covered microhabitats. Foliage in insecticide-treated, open microhabitats had significant decreases in nitrogen, potassium, and phosphorus (Table 6).

In mowed mountain brush habitats, arthropods functioned to restrict the flow of nutrients from foliage to litter or, conversely, to accelerate the flow of nutrients from litter to foliage. Earlier work on sagebrush habitats showed that insects are critical components in the process of litter decomposition (Christiansen and Lockwood, unpublished data). Thus, we suggest that the application of insecticides decreased the breakdown of litter by arthropods and thereby reduced the nutrients available to plants. The fact that arthropods apparently had the opposite effect on mobilization of nutrients in mowed and herbicide-treated habitats may have been a result of the functional differences in these treatments; the overstory plants were rapidly recovering following mowing but were effectively eliminated by herbicide applications.

Burning a habitat dramatically altered the plant architecture, leaving no closed microhabitats. In burned sites treated with insecticides, magnesium, potassium, and phosphorus were all significantly increased in litter (Table 7). As with mowing, significant nutrient increases in litter indicate that insects are important in mobilizing nutrients. Burned habitats had properties of herbicide-treated habitats (elimination of the canopy) and mowed habitats (ongoing recovery of the overstory plants, although insufficient for sampling). Plants under various stresses respond differently (Hale and Orcutt 1987), and it is not unexpected that the interacting impacts of arthropods and management practices resulted in different alterations in nutrient cycling.

ACKNOWLEDGMENT

We thank C. C. Burkhardt for assistance with pesticide applications and P. Lew for field and laboratory assistance. This project was partially funded by USDA-CSRS grant 85-CSRS-2-2702.

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LOCALITY, HABITAT, AND ELEVATION RECORDS FOR THE DESERT SHREW, *NOTIOSOREX CRAWFORDI*

Russell Davis[1] and Ronnie Sidner[1]

ABSTRACT.—Two specimens of *Notiosorex crawfordi* (Coues) were obtained from the Rincon Mountains in southeastern Arizona. Elevations were 2,438 and 2,618 m. At the lower-elevation site the habitat was a meadow in a ponderosa pine forest.

The desert shrew, *Notiosorex crawfordi* (Coues), is known to occur in a wide variety of habitats ranging from desert gravel to ponderosa-pinyon pine woodlands, and at elevations from sea level to 2,100 m (Armstrong and Jones 1972).

On 14 August 1985, while trapping rodents on top of Spud Rock (elevation 2,618 m by bench mark) in the Rincon Mountains of Saguaro National Monument near Tucson, Arizona, we found a dead specimen of this shrew. While there is not much vegetation on the top of Spud Rock itself, it is surrounded below by a fir forest to the north and east and a ponderosa pine (*Pinus ponderosa*) forest to the south and west (Marshall 1956).

The dead shrew was lying exposed on a large rock, and the skin was dry with some minor damage (the skull was partially exposed). This suggested the possibility that this individual might have been caught by an owl or other predator in a lower-elevation habitat and carried to this site. A 32-km radius should encompass virtually the entire area from which the prey of raptors would be obtained, and most prey are taken within 5 km of a site (Harris 1977). But in this case, because of local topography in this small mountain range, these distances (whether considered horizontally or vertically) could extend through habitats ranging from desert shrub to montane conifer forest.

During early summer of 1985 we placed 25 plastic can traps in a grass-fern meadow that was surrounded by ponderosa pines near Manning Camp (elevation 2,438 m by Park Service sign), about 2 km south of the Spud Rock site. These can traps, with holes in the bottoms for drainage, were checked in late summer 1985 and early summer 1986 without success. They then remained unattended until removed on 2 June 1988. At that time one of the traps, located adjacent to a rotting log in a dry, grassy portion of this meadow, contained a decomposed specimen of *Notiosorex crawfordi*, the only mammal caught in these traps throughout the three-year period.

This specimen establishes the fact that a small population of the desert shrew does occur at least in one meadow within a ponderosa pine forest in these mountains. If an owl (or other predator) were responsible for the other specimen found dead on Spud Rock, it may not have been carried for any appreciable distance nor was it necessarily obtained from some habitat different from that occurring near its discovery site.

Findley (1969) has shown that *Tamias dorsalis* occurs from the bottom to the top of certain southwestern mountains in the absence of other species of chipmunks (as is the case in the Rincons), but that it is restricted to lower portions when these species are present. Perhaps the elevational and habitat distribution of *Notiosorex crawfordi* expands comparably in the absence of other species of shrews.

Rodents collected at both study sites include *Sigmodon ochrognathus* (see Davis and Ward 1988), *Peromyscus boylii*, and *Neotoma mexicana*. Whitetail deer (*Odocoileus virginianus*) and 14 species of bats occasionally occur in the meadow, pocket gopher mounds are abundant, and *Sciurus aberti*, *Spermophilus variegatus*, and *Tamias dorsalis* have been seen in the vicinity. Except for the two specimens reported here, no other shrews are known from the Rincon Mountains.

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Acknowledgments

S. P. Cross suggested the can traps, and O. G. Ward helped in putting them out. E. L. Cockrum verified the identification of the two specimens. This study was possible only with logistic help from Park Service personnel at Saguaro National Monument.

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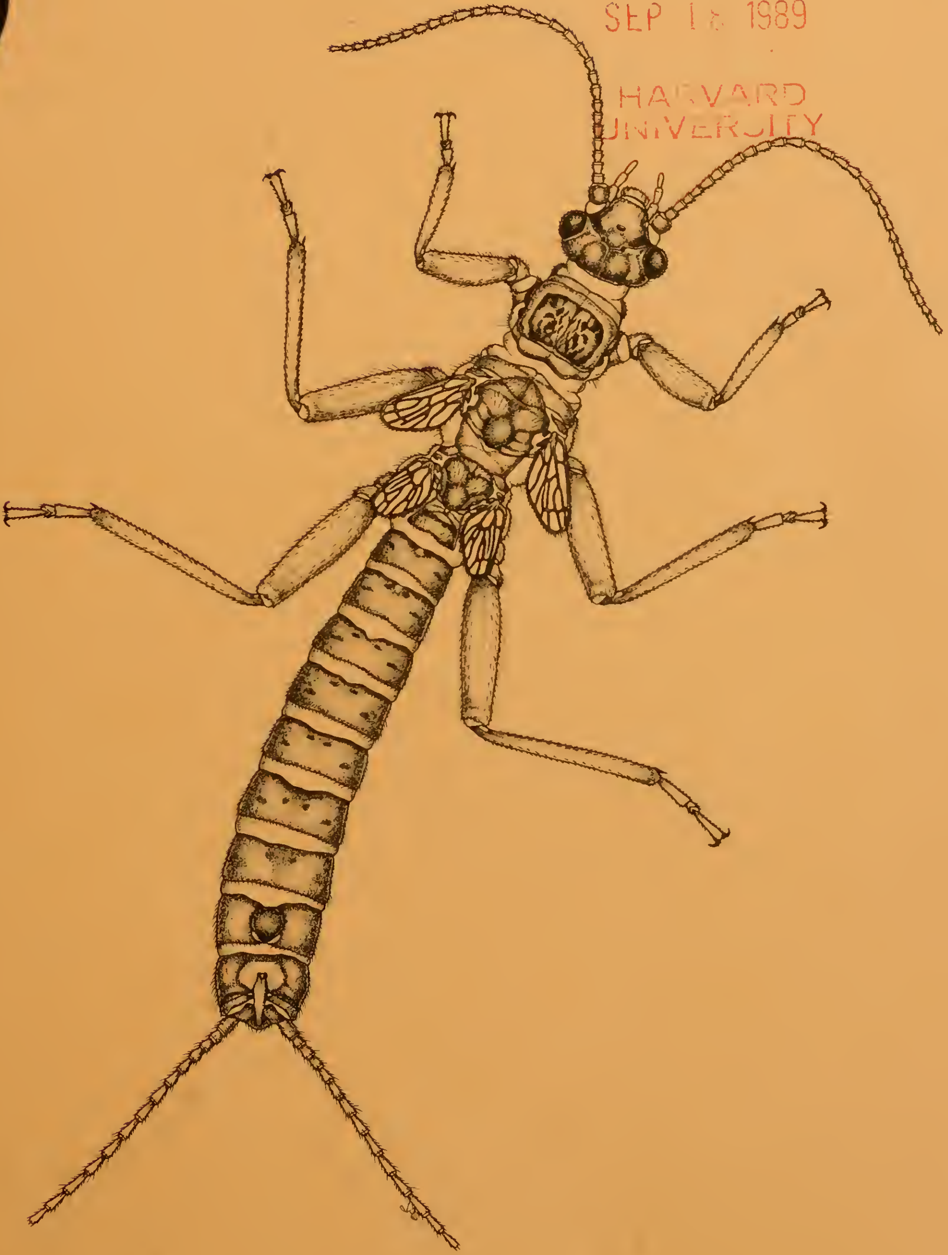

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7-89 650 40815

ISSN 017-3614

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 49 30 April 1989 No. 2

SNAKE CREEK BURIAL CAVE AND A REVIEW OF THE QUATERNARY MUSTELIDS OF THE GREAT BASIN

Emilee M. Mead[1,3] and Jim I. Mead[1,2,3]

ABSTRACT.—Snake Creek Burial Cave (SCBC), east central Nevada, is a unique paleontological deposit. The cave is the first natural trap excavated in the Great Basin and one of the few localities describing a valley-bottom community. The recovery of extinct *Camelops* sp. (camel) and *Equus* spp. (horse), in addition to radiometric dates, indicates at least some of the deposits to be of late Pleistocene age. Eight mustelid species have been identified from SCBC, including three species not previously reported from the late Rancholabrean of the Great Basin: *Mustela nigripes* (black-footed ferret), *M. nivalis* (least weasel), and *Gulo gulo* (wolverine). A review of late Pleistocene deposits indicates that there are more species of mustelids recovered from Snake Creek Burial Cave than from any other locality in the Great Basin.

The Great Basin of western North America encompasses some 390,000 km^2 and, although centered in Nevada, also extends into several adjoining states (Fig. 1). This arid region is generally characterized by linear, north-south trending mountain ranges, separated by closed-drainage valleys (Hunt 1967). A number of archaeological and paleontological sites have been excavated in the Great Basin. Few, however, have contained lengthy, well-dated, stratified sequences extending from the Pleistocene, across the critical Pleistocene-Holocene boundary, and into the Holocene. Futhermore, those few sites meeting these criteria have generally been restricted to the mountainous peripheries (Grayson 1987), leaving the valley-bottom communities largely undescribed. Since small mammals are generally sensitive to environmental change, their recovery in archaeological and paleontological sites can provide important paleoenvironmental data. Snake Creek Burial Cave (SCBC), White Pine County, east central Nevada, has recently been excavated; an estimated 30,000 fish, amphibian, reptilian, avian, and mammalian bones have been recovered. Of particular interest are the many carnivore remains, including numerous mustelids (Order Carnivora: Family Mustelidae; weasel family). This paper provides a brief description of SCBC, including recovered mustelids, as well as a timely review of other localities in the Great Basin reporting fossil or subfossil mustelids. A detailed osteological report of all carnivores recovered from SCBC is in progress. Additional reports describing the avian and remaining mammalian remains are forthcoming.

SNAKE CREEK BURIAL CAVE

Setting

Snake Creek Burial Cave is a unique paleontological deposit. The natural trap cave, with a sinkhole depression and a 17-m, vertical, free-fall entrance (Fig. 2), is located at an elevation of 1,731 m on a small limestone

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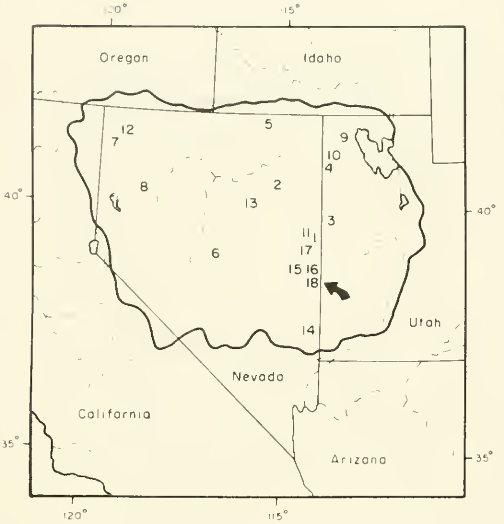

Fig. 1. Location map indicating the extent of the Great Basin (heavy line; after Küchler 1966); fossil and subfossil locality numbers correspond to those in Table 1.

ridge (Devonian-age Guilmette Formation) in the midst of a bajada developed from the drainage of Snake Creek, southern Snake Range (Figs. 1, 3). When pluvial Lake Bonneville was at its highest stand during the Wisconsinan glacial (16,000 to 13,000 yr B.P.; Thompson et al. 1986), the beach was within 5 km to the northeast of the cave. SCBC lies directly in a Pleistocene north-south trending habitat corridor that extends from Idaho to northern Arizona and is bordered by numerous mountain ranges, including the Snake Range, and by the Bonneville lake system.

SCBC allows a description to be made of the late glacial vertebrate community that occurred in a valley bottom along the lake margin, an as yet inadequately described biome. The remains are from a natural trap cave; no other caves of this type have been excavated in the central Great Basin. A high proportion of carnivores was recovered from SCBC, in addition to an excellent record of other small and large animals. Natural trap cave localities have traditionally recorded a different faunal sequence from those in walk-in caves, open-air sites, raptor roosts, or packrat middens (White et al. 1984).

Methods

Just as SCBC is currently accumulating faunal material, so too in the past did animals fall into the natural trap and die. It is certain that accumulation has been occurring since at least late Pleistocene (Rancholabrean) time. Included in the 30,000 bones are remains of the extinct *Camelops* sp. (camel) and *Equus* spp. (horse). The deposits are of an undetermined depth; at 120 cm below the floor surface, faunal remains were still recovered in good quantity.

Five 1-m^2 units were excavated, all to a depth of approximately 1 m below present floor surface (Fig. 4). An initial 1 × 1-m test pit was excavated in 1984, and four additional units were excavated in 1987. All units were excavated in 10-cm arbitrary levels since the natural stratigraphic levels were all deeper than 10 cm. All material was screened through both 5-mm and 1-mm screens.

STRATIGRAPHY.—SCBC is commonly visited by spelunkers. Consequently, some disturbance of the sediments has occurred as the cavers have dug in search of additional cave passage. Unit I of the excavated sediment is not of primary deposition. Rather, it retains the mottled appearance of mixed sediment and represents the backdirt of the cavers' diggings from nearby areas in the cave. Specimens recovered from this unit (I) are used only in a presence-absence status, not in any chronosequence of events. A bat guano layer was encountered below the disturbed unit and is referred to as Unit II. This dung layer is 100% bat guano with no mixing; therefore, we infer that primary deposition begins with Unit II, that is, the bat guano and all sediment below it (Unit III) are in natural stratigraphic sequence.

Three radiometric dates have been secured on materials in situ from the excavation. A conventional radiocarbon date of 7,860 ± 130 yr B.P. (Beta-22169) was obtained directly on the bat guano (Unit II). The Accelerator Mass Spectrometry (AMS) radiocarbon technique was used on a small piece of wood recovered from the very top of Unit III; the date is reported as 9,460 ± 160 yr B.P. (Beta-24643, ETH-3688). A U-Th (uranium-thorium; performed by Dr. Richard Ku, University of Southern California) series date on an *Equus* second phalanx recovered from near the bottom of our excavations in Unit III is 15,100 ± 700 yr B.P. Figure 5 is a schematic stratigraphic section illustrating the proposed stratigraphic relationships including the radiometric dates.

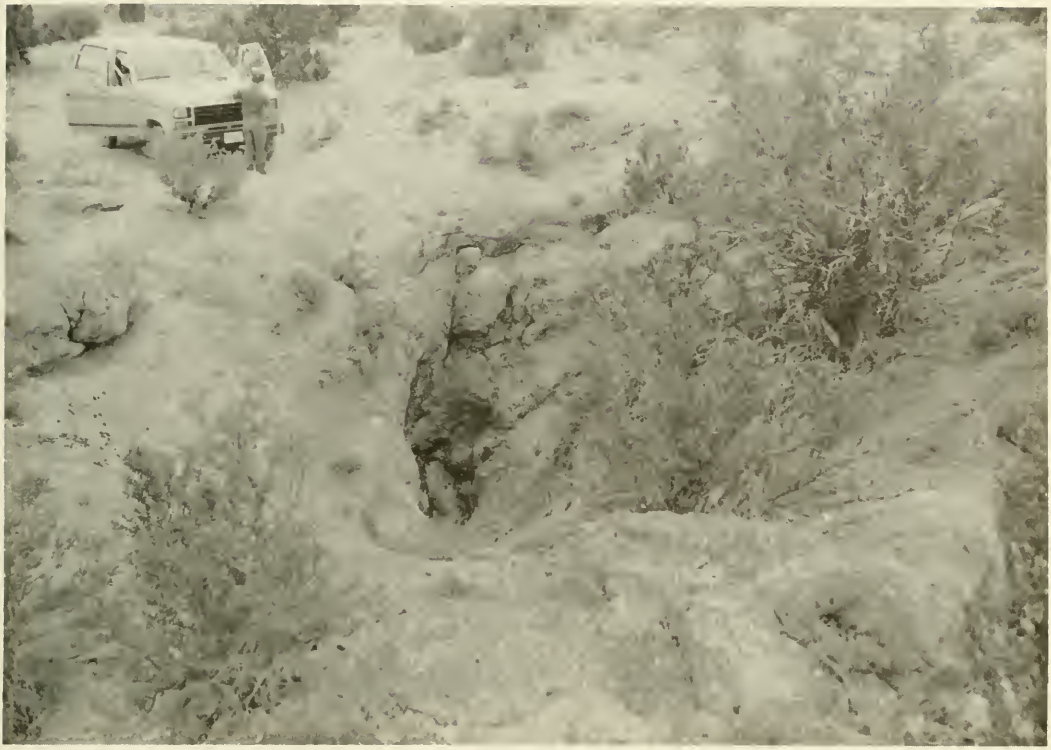

Fig. 2. Entrance to Snake Creek Burial Cave.

Recovered remains.—Eight species of mustelids have been recovered from SCBC, including three species not previously reported from late Rancholabrean localities in the Great Basin: *Mustela nigripes* (black-footed ferret), *M. nivalis* (least weasel), and *Gulo gulo* (wolverine). The implications of these mustelid reports are discussed. The diversity of identified mustelid species from SCBC is higher than that from any other locality in the Great Basin. Table 1 provides a list of those localities in the Great Basin reporting fossil or subfossil mustelid remains. Reports from a majority of the sites include only one or two mustelid species (Hidden Cave and Smith Creek Cave both report six, the most after SCBC). However, some 18 localities are now reporting fossil or subfossil mustelids. Figure 1 illustrates the geographic locations of these 18 sites; the arbitrary site numbers correspond to the numbers assigned in Table 1.

Also included is a review of the fossil and subfossil mustelid localities in the Great Basin.

Descriptive Accounts

Martes americana
American marten

Map localities.—2, 3, 5, 18.

Discussion.—*Martes americana* generally prefers mature conifer or mixed-forest stands with greater than 30% canopy cover, although meadows are often used in the summer if more food is available there. The American marten is an opportunistic feeder that takes advantage of local and seasonal abundances. While *Clethrionomys* spp. (red-backed vole), *Microtus* spp. (meadow vole), *Lepus americanus* (snowshoe hare), and *Tamiasciurus* spp. (tree squirrels) are favored foods, fruits and insects can play a significant role in the diet (Ewer 1973, Strickland et al. 1982, Clark et al. 1987).

Martes americana is reported from four fossil localities in the central Great Basin. However, one of the two specimens from Bronco Charlie Cave (Spiess 1974) has been reassigned to *M. nobilis* (Grayson 1987) and is

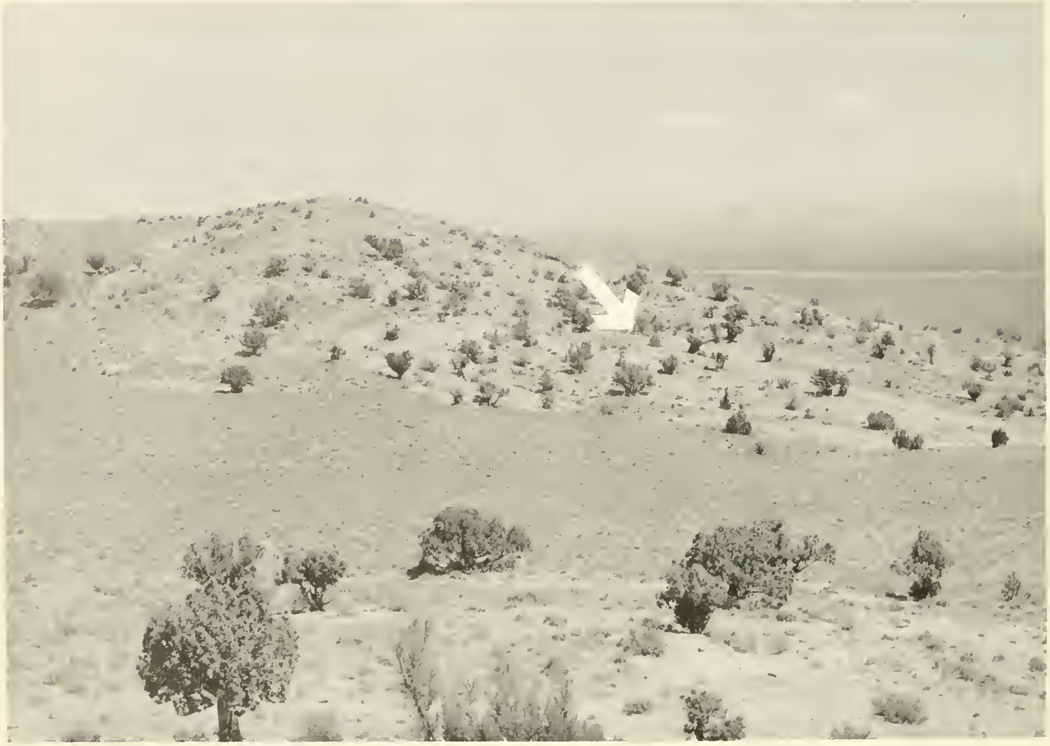

Fig. 3. SCBC is located by the arrow. The valley bottom (pluvial Lake Bonneville) is clearly visible in the background.

discussed in that section. The other specimen remains undetermined.

Crystal Ball Cave, Deer Creek Cave, and Snake Creek Burial Cave are all outside the modern range of *M. americana*. Figure 6 identifies the fossil sites of *M. americana*, *M. nobilis*, and *Martes* sp. in the arid West and illustrates the modern geographic range of *M. americana*. The American marten currently ranges in the Sierra Nevada and the Rocky Mountains, but it does not occur on mountain ranges within the Great Basin. However, until more precise environmental and chronological guidelines are found that distinguish *M. americana* from *M. nobilis* localities, most paleoecological interpretations should be considered tentative.

Martes nobilis
Extinct noble marten

MAP LOCALITIES.—2, 8, 17, 18.

DISCUSSION.—*Martes nobilis* has been reported from three fossil localities in addition to the reassignment of the Bronco Charlie specimen (Fig. 6). Anderson (1970) provides measurements and morphological characters of the cranium and dentition used to distinguish the species. Anderson (1970: 85) states, "I do not believe that *M. nobilis* was related to *M. americana*," and that competition with the American marten, a warming climate, and perhaps the activities of man caused the extinction of the noble marten. Until recently, *M. nobilis* was thought to have become extinct at the end of the Pleistocene and perhaps to have adapted to cooler conditions. Grayson (1987), however, reports three localities in the arid West, two from the Great Basin, with noble marten remains dating into the late Holocene: (1) Dry Creek Rockshelter, southwestern Utah, 3,270 ± 110 yr B.P.; (2) Hidden Cave, Nevada, 3,600–3,700 yr B.P.; and (3) Bronco Charlie Cave, Nevada, 3,500 yr B.P. If we assume these dates are accurate in their associations, we see no clear reason why *M. nobilis* survived terminal Pleistocene environmental changes and then became extinct in the late Holocene. Clearly, additional research is required. Only at SCBC is there an indication that both species may have occurred together in the Great Basin.

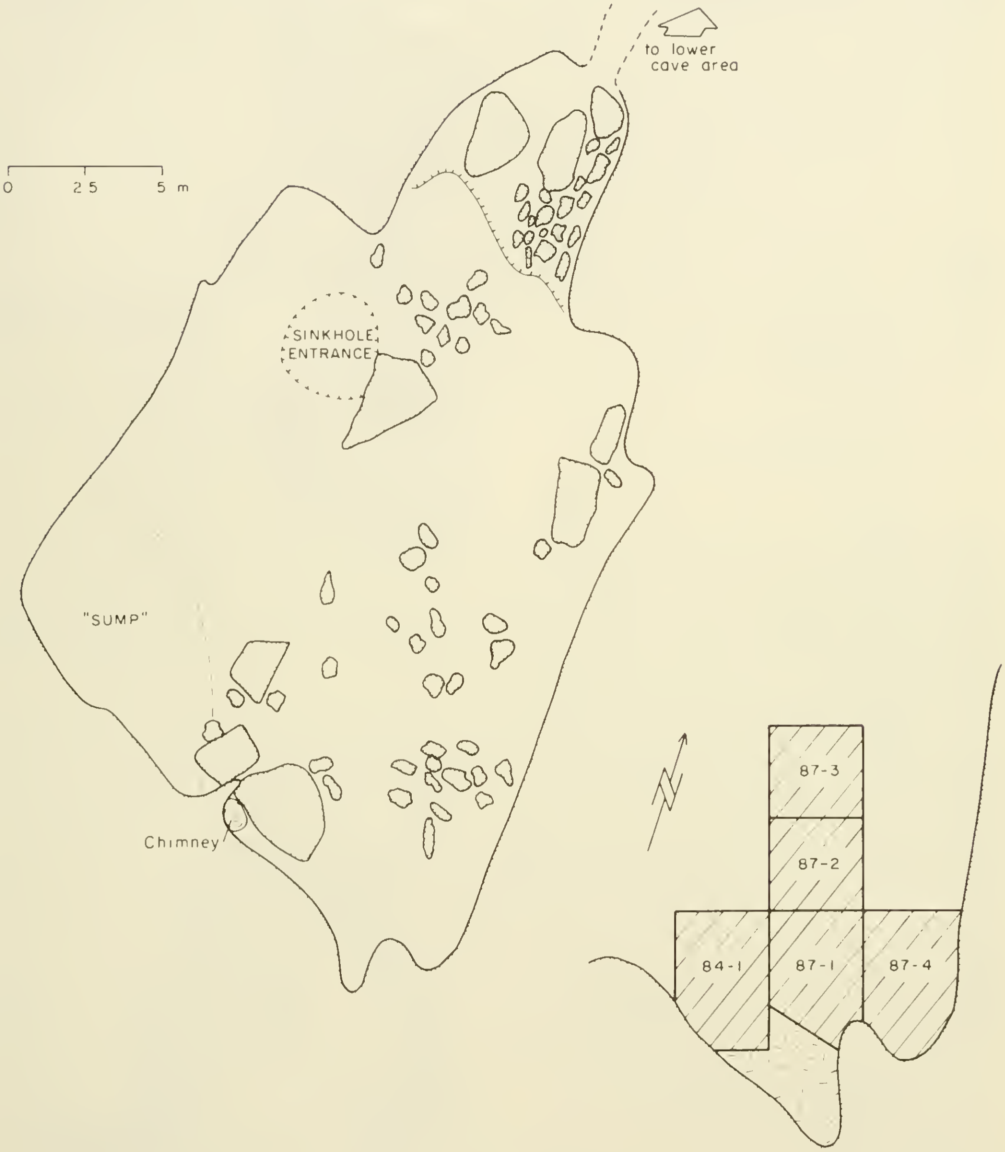

Fig. 4. Plan view of SCBC with the excavation units enlarged.

Martes sp. is reported from two localities, Hidden and Smith Creek caves (8, 17) (Fig. 6). The Hidden Cave specimens are all postcranial elements, and Grayson (1985) does not definitely distinguish them as either *M. americana* or *M. nobilis*. The Smith Creek Cave specimen was first identified by Goodrich (1965) as *Martes* sp. and further reported by Miller (1979), who made no further identification.

Mustela erminea
Ermine

MAP LOCALITIES.—15, 17.

DISCUSSION.—Ermines generally inhabit a variety of boreal habitats, although they tend to avoid dense coniferous forests and deserts. The diet of *M. erminea* consists primarily of small mammals, especially *Microtus* spp., *Blarina* spp. (short-tailed shrew), and *Peromyscus* spp. (deer mouse) (Ewer 1973,

TABLE 1. Fossil and subfossil mustelid localities reported from the Great Basin. Site numbers are arbitrary designations and correspond to the numbers on Figure 1. X = fossil/subfossil, in vicinity today; * = extirpated; ! = extinct.

Locality number	Locality name	*Martes americana*	*Martes nobilis*	*Martes* sp.	*Mustela erminea*	*Mustela frenata*	*Mustela nigripes*	*Mustela nivalis*	*Mustela vison*	*Mustela* sp.	*Gulo gulo*	*Taxidea taxus*	*Brachyprotoma brevimala*	*Mephitis mephitis*	*Spilogale putorius*	*Spilogale* sp.	Primary reference(s)
1	Amy's Rockshelter											X					Miller 1979, Mead et al. 1982
2	Bronco Charlie	*	![1]			X									X		Spiess 1974
3	Crystal Ball Cave	*				X			*				!				Heaton 1985
4	Danger Cave					X						X					Jennings 1957, Grayson 1988
5	Deer Creek Cave	*															Ziegler 1963
6	Gatecliff Shelter													X	X		Grayson 1983
7	Hanging Rock Shelter					X						X					Grayson and Parmalee 1988
8	Hidden Cave		!	X		X			X	X		X		X	X		Grayson 1985
9	Hogup Cave					X				X		X			X		Aikens 1970
10	Juke Box Cave														X		Jennings 1957
11	Kachina Cave											X					Miller 1979, Mead et al. 1982
12	Last Supper Cave					X				X[2]		X		X	X		Grayson 1988
13	Mineral Hill Cave									X		X				X	McGuire 1980
14	O'Malley Shelter											X					Fowler et al. 1973
15	Owl Cave #1				X												Turnmire 1987
16	Owl Cave #2											X					Turnmire 1982
17	Smith Creek Cave		!	*	X	X			*	X		X			X	X	Miller 1979, Mead et al. 1982
18	SNAKE CREEK BURIAL CAVE	*	!			X	*	*			*	X			X		This report

[1] See Grayson 1987.

[2] Possibly *M. erminea*; see discussion in text

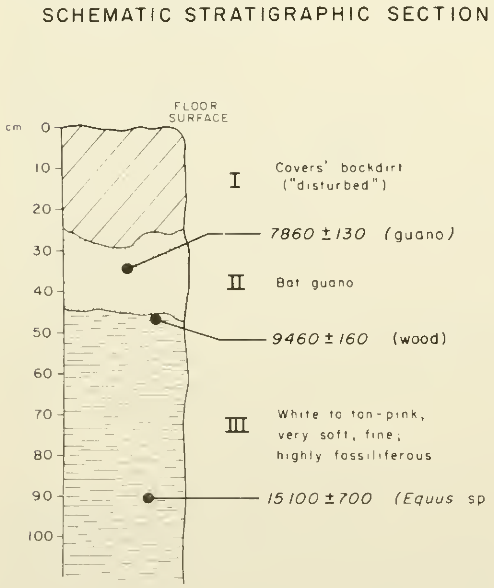
SCHEMATIC STRATIGRAPHIC SECTION
FLOOR SURFACE
cm
0
10
20
30
40
50
60
70
80
90
100
I
Covers' backdirt ("disturbed")
7860 ± 130 (guano)
II
Bat guano
9460 ± 160 (wood)
III
White to tan-pink, very soft, fine; highly fossiliferous
15100 ± 700 (Equus sp.)

Fig. 5. Schematic stratigraphic section from SCBC, with associated radiometric dates.

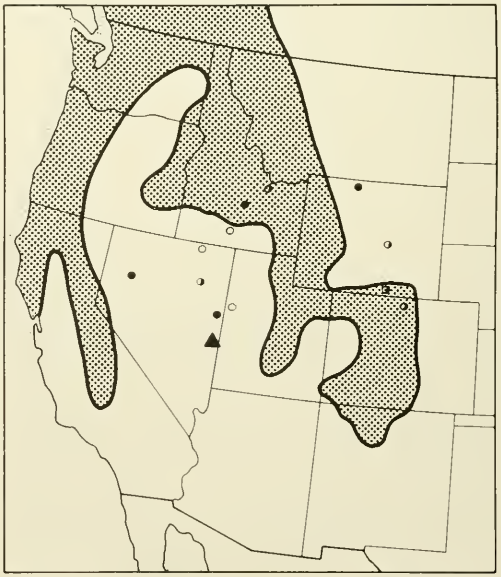

Fig. 6. Modern distribution of *Martes americana* (shaded area) with fossil and subfossil localities of *M. americana* (○) and *M. nobilis* (●); ▲ = SCBC.

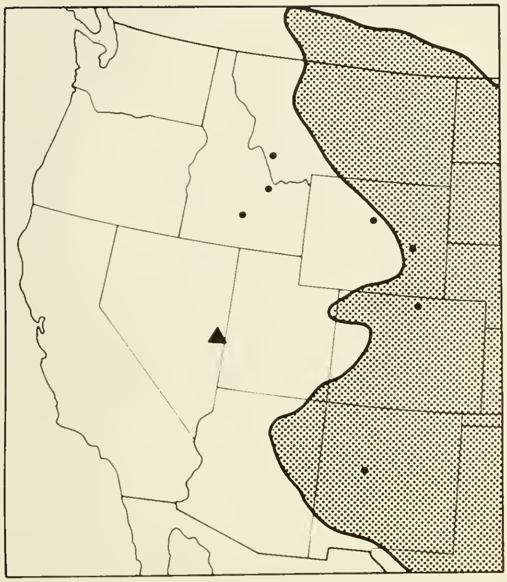

Fig. 7. Map indicating the historic distribution of *Mustela nigripes* (shaded area) with fossil and subfossil localities (●); ▲ = SCBC.

Svendsen 1982). Only two confirmed fossil records are reported from the Great Basin, Owl Cave #1 and Smith Creek Cave, both in the Snake Range, eastern Nevada. Grayson (1988) reports an innominate assigned to *Mustela* sp. from Last Supper Cave, northwestern Nevada. While conclusive evidence does not allow a definitive assignment, the specimen most likely represents *M. erminea* rather than *M. frenata* as reported by Grayson (1988).

Brown (1978) defined boreal habitats in the Great Basin as those above 2,290 m elevation, well above the elevation of SCBC. If boreal mammals colonized the Great Basin during the Pleistocene and became isolated on, or extirpated from, the Great Basin mountains during the Holocene, then boreal mammals must have at one time occupied lowland areas (Brown 1978, Grayson 1987). *Mustela erminea* currently inhabits the boreal regions of the Snake Range and several other mountain ranges of the Great Basin. However, Owl Cave #1 (1,700 m), Smith Creek Cave (1,950 m), and Last Supper Cave (1,646 m) are all below the present boreal limit as established by Brown (1978) and would, therefore, support his hypothesis.

Mustela frenata
Long-tailed weasel

MAP LOCALITIES.—2, 3, 4, 7, 8, 9, 12, 17, 18.

DISCUSSION.—Long-tailed weasels are fairly ubiquitous today and can be found in virtually every habitat from tropical areas to arctic alpine. *Mustela frenata* mostly eats small rodents, particularly *Microtus* spp., while birds, insects, and plant material are rarely consumed. Their distribution is presently limited only by summer water availability (Ewer 1973, Svendsen 1982). All nine reported fossil localities in the central Great Basin occur within the modern geographical distribution of *M. frenata*.

Mustela nigripes
Black-footed ferret

MAP LOCALITY.—18.

DISCUSSION.—This Snake Creek Burial Cave fossil is the first report of the black-footed ferret from the Great Basin. *Mustela nigripes* is currently an endangered species, and even the historic distribution does not place the ferret as far west as eastern Nevada (Fig. 7). The closest fossil locality to SCBC is Moonshiner Cave, Idaho (Anderson 1974).

The black-footed ferret, which currently occupies short- and mid-grass prairies, is closely associated with *Cynomys* (prairie dog), depending upon it for food as well as utilizing the prairie dog burrows for shelter and travel (Svendsen 1982, Nowak and Paradiso 1983). Although *Cynomys* has not been recovered from SCBC, *Marmota* (marmot) and other colonial ground squirrels (e.g., *Spermophilus townsendii*) are common.

Mustela nivalis (= *rixosa*)
Least weasel

MAP LOCALITY.—18.

DISCUSSION.—*Mustela nivalis*, the smallest living carnivore, inhabits marshy areas including meadows, cultivated fields, and open woodlands. Rodents, primarily *Microtus* spp., form the staple diet for the least weasel; however, shrews are also often a favored prey (Ewer 1973, Svendsen 1982). Snake Creek Burial Cave, east central Nevada, is the first reported fossil locality of *M. nivalis* in the Great Basin. Moonshiner Cave, Idaho (Anderson 1974), is the only other reported fossil locality in the western United States; both

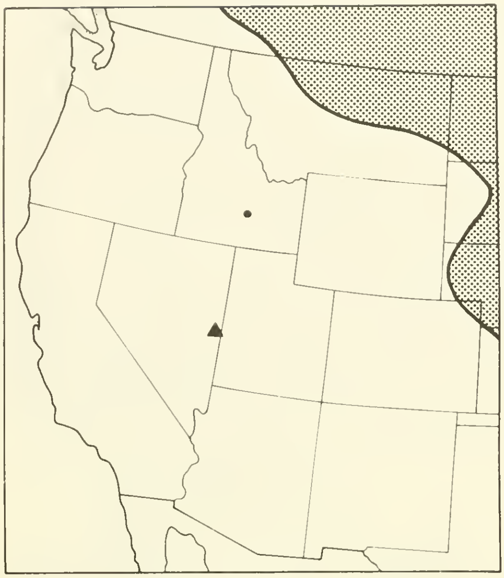

Fig. 8. Modern distribution of *Mustela nivalis* (shaded area); ● = Moonshiner Cave, Idaho (Anderson 1974); ▲ = SCBC.

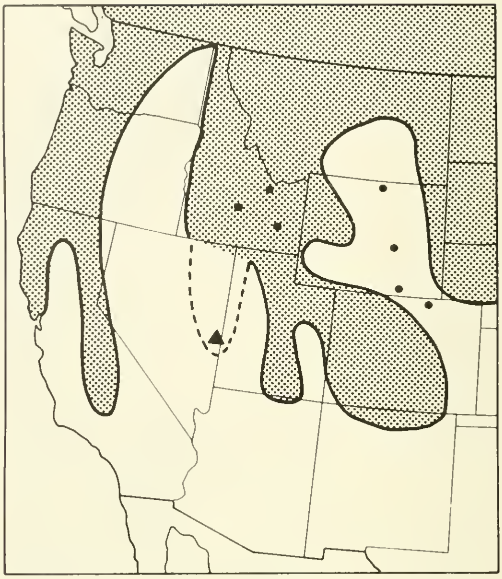

Fig. 9. Modern distribution map of *Gulo gulo* (shaded area). Dashed line indicates the range extension proposed by Hall (1981). Fossil localities are indicated (●); ▲ = SCBC.

localities are well outside the current distributional range of the least weasel (Fig. 8).

Mustela vison
Mink

MAP LOCALITIES.—3, 8, 17.

DISCUSSION.—The mink inhabits wetlands of all kinds including river banks, streams, and swamps. The diet of *M. vison* is quite variable by season and geographical location and can include insects, crustaceans, fish, amphibians, reptiles, and small mammals (Ewer 1973, Linscombe et al. 1982). Three fossil localities report *M. vison* in the central Great Basin, Crystal Ball Cave, Utah, and Hidden Cave and Smith Creek Cave in Nevada. The mink is known to currently inhabit the area near Hidden Cave (northwestern Nevada); however, it is extirpated from the Snake Range (Crystal Ball and Smith Creek caves).

The recovery of fossil *M. vison* from Crystal Ball and Smith Creek caves is not surprising due to the close proximity of these caves during the Pleistocene to either riparian (Smith Creek Cave) or lakeshore (Crystal Ball Cave) environments. With the recovery of *M. nigripes* from SCBC, and because of some osteological similarities with mink, all *M. vison* material reported from the Great Basin should be reexamined.

Mustela sp. is reported from five localities in the Great Basin (8, 9, 12, 13, 17). As discussed, the specimen reported from Last Supper Cave (Grayson 1988) may be assignable to either *M.* cf. *erminea* or *M.* cf. *frenata*, but it is too small to be either *M. vison* or *M. nigripes*.

Gulo gulo (=*luscus*)
Wolverine

MAP LOCALITY.—18.

DISCUSSION.—SCBC is the only reported locality of *Gulo* in the central area of the Great Basin (Barker and Best 1976), although one was killed in 1900 in the Wasatch Mountains in Utah. Based solely upon this undated specimen, Hall (1981) extended the modern range of the genus into the Snake Range (Fig. 9). However, since extinct fauna (*Camelops* and *Equus*) have been recovered from the surface of SCBC (cavers' backdirt, this report), presence alone cannot determine the age of the specimen. Without directly dating the SCBC specimen, it is impossible to unequivocally determine if the wolverine cranium is modern or fossil.

TABLE 2. Observed ranges, means, and standard deviations of modern *Gulo gulo;* measurements of the Snake Creek Burial Cave specimen; and observed ranges and means of Pleistocene *Gulo* specimens (Anderson 1977). All measurements in mm.

	Modern specimens (n = 16)			Snake Creek Burial Cave	Anderson F:AM	
Measurement	Observed range	Mean	S.D.		Observed range	Mean
Length C-M1*	45.73– 52.58	49.93	2.21	56.00	51.3– 62.8	57.72
Length P2-M1*	35.05– 43.08	39.60	2.32	44.04		
Length C1*	10.16– 13.48	11.83	0.99	14.00		
Width C1*	7.96– 10.78	9.28	0.90	11.50		
Width M1	11.69– 15.18	13.49	1.03	14.67	13.5– 15.8	14.80
Length M1	6.28– 8.19	7.28	0.66	8.15	7.1– 9.0	8.06
Length P4*	17.01– 21.20	19.46	1.28	22.70	21.6– 23.4	22.70
Length P4	18.37– 21.81	20.04	1.12	23.14		
Width P4	9.67– 12.16	10.87	0.82	13.21	12.6– 13.5	12.96
Length P3	9.45– 10.92	10.16	0.47	11.11		
Width C-C	18.16– 23.14	20.36	1.55	22.11		
Width M1–M1	27.92– 33.00	30.63	1.75	34.40		
Mast. breadth	74.96– 93.28	84.95	6.83	96.16	85.0–108.0	96.50
BCL	78.27–138.81	115.62	23.78	143.24	139.4–172.0	155.70

*Measurements by alveolar, all other measurements are tooth measurements

Table 2 presents measurements of the SCBC *Gulo* cranium, several modern specimens, and Pleistocene wolverines from Alaska (Anderson 1977). The SCBC specimen compares very favorably with the Alaskan Pleistocene material and is well outside the range of the modern specimens for most measurements. We suggest that the SCBC specimen is not modern, but late Rancholabrean, and, therefore, that the modern range as suggested by Hall (1981) should be revised.

Taxidea taxus
Badger

MAP LOCALITIES.—1, 4, 7, 8, 9, 11, 12, 13, 14, 16, 17, 18.

DISCUSSION.—The badger occupies a wide variety of habitats and takes advantage of local abundances of terrestrial animals (insects, reptiles, birds, and mammals). *Spermophilus* spp., *Microtus* spp., and insects seem to form the staple diet for *Taxidea* (Ewer 1973, Lindzey 1982). All reported fossil localities of *Taxidea* are within the modern range. As yet, no published accounts indicate that the badger was larger during the late Pleistocene in the Great Basin than it is today.

Brachyprotoma brevimala
Extinct short-faced skunk

MAP LOCALITY.—3.

DISCUSSION.—Crystal Ball Cave, Utah, is the only fossil locality of this extinct genus reported from the Great Basin (Heaton 1985). Heaton (1985) described *B. brevimala* and distinguished it from *B. obtusata* (Conard Fissure, Arkansas; Brown 1908) on the basis of several cranial characteristics. While it is difficult to assign any paleoecological affinities to this extinct skunk, Heaton (1985) and Kurtén and Anderson (1980) indicate that *Brachyprotoma* is always associated with boreal faunas even though other skunk genera are occasionally also recognized at each site. Heaton (1985) further speculates, based on tooth morphologies, that *Brachyprotoma* was more carnivorous than any living skunk.

Mephitis mephitis
Striped skunk

MAP LOCALITIES.—6, 8, 12.

DISCUSSION.—*Mephitis mephitis* lives in a variety of habitats and is omnivorous (Ewer 1973, Godin 1982, Nowak and Paradiso 1983). The striped skunk is reported from three fossil localities, all in northern Nevada and within the modern range of the species.

Spilogale putorius (=*gracilis*)
Spotted skunk

MAP LOCALITIES.—2, 6, 8, 9, 10, 12, 17, 18.

DISCUSSION.—*Spilogale putorius* inhabits a variety of brushy, rocky, and wooded habitats but generally avoids dense forests and wetlands. The spotted skunk is an opportunistic feeder that consumes beetles, worms, crickets, frogs, carrion, and rodents (Ewer 1973, Howard and Marsh 1982, Nowak and Paradiso

1983). None of the eight reported fossil localities of *S. putorius* is outside the modern range. However, with the report of *Brachyprotoma*, an extinct skunk approximately the size of *Spilogale*, from Crystal Ball Cave, caution should be used in examining fossil skunk material from the Great Basin.

Spilogale sp. is reported from two localities (13, 17); these specimens probably represent *S. putorius*.

DISCUSSION AND CONCLUSIONS

The Rancholabrean paleontological history of the Great Basin of western North America is largely unstudied. The region has provided a variety of diverse habitats through time, from valley to mountainous communities, including compressed zones resulting from mountain glaciations and pluvial lakes Bonneville and Lahontan in the Pleistocene. The Great Basin has been, and continues to be, a dynamic system recording fluctuating climatic conditions with lengthy paleobotanical and paleontological records. However, it has been only in the last few years that these records have been studied.

Small mammals are sensitive to environmental change, and, therefore, their recovery from archaeological and paleontological sites can provide important paleoenvironmental data. SCBC has provided a unique situation in Great Basin paleontology, a deeply stratified, natural trap deposit representing a valley-bottom community. The mustelid species diversity at SCBC exceeds any other reported locality in the Great Basin (Table 1) and includes three late Rancholabrean-age species not previously reported as fossil from the region: *Mustela nigripes*, *M. nivalis*, and *Gulo gulo*.

The recovery of a *Gulo* cranium (Barker and Best 1976) from SCBC led Hall (1981) to extend the modern range of the genus into the Snake Range. Measurements of the SCBC specimen were compared with modern specimens and with Pleistocene wolverines from Alaska (Anderson 1977). We believe, based upon these measurements and on radiometric analyses of the cave fauna, that *Gulo* is not present today in eastern Nevada but, rather, that the specimen represents a fossil occurrence, the first in this part of the Great Basin.

Several discoveries unique to SCBC have led us to further refine the hypotheses concerning vegetational communities in the valley bottoms of the central Great Basin during the last glacial. Brown (1971, 1978) proposed that, based upon the relictual appearance of boreal mammals on certain "island" mountain ranges, the valley bottoms must have contained a continuous woodland or forest corridor from the Rocky Mountain "mainlands" to eastern Nevada. Wells (1983) examined *Neotoma* (packrat) middens and proposed that stands of the subalpine *Pinus longaeva* (bristlecone pine) occurred down to 1,660 m elevation (as late as 11,880 yr B.P.), close to the high beach stands of Lake Bonneville, where the species probably mixed into a mosaic community with *P. flexilis* (limber pine). Thompson and Mead (1982) recovered a *Neotoma* midden at 1,640 m elevation; from this record they hypothesized that subalpine stands of *P. flexilis* occurred at low elevations near the lake on rocky, calcareous substrates. Deep alluvial deposits in the valley bottoms (and away from *Neotoma* scavenging) were probably vegetated by shrub and/or meadow communities (Thompson and Mead 1982). Mead et al. (1982) analyzed a variety of faunas, including Smith Creek Cave (1,950 m elevation), from the nearby Snake Range. While many boreal and mountain species were recovered, the discoveries of Rancholabrean-age *Crotaphytus wislizenii* (=*Gambelia;* leopard lizard) and *Phrynosoma platyrhinos* (desert horned lizard) were anomalous. These two species indicate that an open, sparse vegetation community was in existence, possibly along the lake margins, a community not yet thoroughly examined (Mead et al. 1982).

The recovery of *Mustela nigripes* from SCBC seems to corroborate the open, sparse community hypothesis, at least near the lakeshore. *Mustela nigripes* generally feeds on *Cynomys*, *Spermophilus* spp., and lagomorphs (rabbits and pikas), while the closely related *M. eversmanni* (Siberian polecat; European ferret) eats a variety of small mammals including *Ochotona* (pika), *Microtus*, and *Marmota* (Anderson et al. 1986). Although *M. nigripes* is currently a near obligate with the prairie dog, in the past the black-footed ferret may have interacted with other colonial ground squirrels, any of which would require at least some open, possibly grassland areas. Interestingly, ground squirrels and lagomorphs (including pikas) are the most abundant species in the SCBC deposit.

Is this near-shore area also the community used by the noble marten? SCBC is the only locality in the Great Basin to report the occurrence of both *Martes americana* and *M. nobilis*. If *M. nobilis* is a valid species, it is possible that these two species had overlapping ranges and yet occupied different niches. Unfortunately, the mystery still remains: How did these animals coexist for such a long period of time and what caused the abrupt extinction of *M. nobilis* 3,000–4,000 years ago? Further, *Mustela nivalis* currently occupies open woodlands, meadows, and cultivated field areas that during the Pleistocene were presumably in the valley bottoms away from rocky substrates. Assuming the behavior of the least weasel was similar in the past to its current behavior, we must conclude again that some open vegetation communities must have been in existence.

We propose that the SCBC deposits and other scattered data (e.g., Crystal Ball Cave) imply that the valley-bottom vegetational communities of the central Great Basin adjacent to the Lake Bonneville beach areas were open, possibly with some grasslands. It is here, in what we would assume was probably a narrow zone along the lake region, that *Mustela nigripes*, *M. nivalis*, possibly *Martes nobilis*, and *Brachyprotoma brevimala* lived on other open-land species such as certain lagomorphs, colonial ground squirrels, and desert lizards. Further work in the valley-bottom habitats will permit a more refined reconstruction.

ACKNOWLEDGMENTS

Financial support for this project was provided by the National Geographic Society (#3627-87, JIM and EMM), the Geological Society of America (#3829-87, EMM), and the Quaternary Studies Program (Northern Arizona University) Mini-Grant Program (EMM). We are grateful to the Bureau of Land Management (BLM), particularly John Zancanella and Shaaron Netherton (Ely District Office) and Lynda Armentrout (Nevada State Office), for their assistance in obtaining permits and for their enthusiastic support of this project. We especially thank A. Cartwright, D. Cartwright, D. Dawson, S. Emslie, W. J. Marsh, J. W. Marsh, C. Mead, and P. Youngman for their assistance in the field. Rita, Chuck, Goodie, and Dave of Baker, Nevada, provided generous help throughout the project. We thank R. Bonnichsen and M. Sorg (Center for the Study of the First Americans, University of Maine), S. McFarlane (BLM), and D. Tuohy (Nevada State Museum). The American Museum of Natural History personnel (New York, New York) and the United States National Museum, particularly B. Fisher (Washington, D.C.), greatly aided our study of modern species. We appreciate the support of L. Agenbroad (Quaternary Studies Program, Northern Arizona University) and R. Foust and H. Hooper (Bilby Research Center, Northern Arizona University).

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DIATOM FLORA OF MINK CREEK, IDAHO, USA

Christopher T. Robinson[1] and Samuel R. Rushforth[2]

ABSTRACT.—Diatoms were collected from an open-canopy and closed-canopy site on Mink Creek, Bannock County, Idaho, a third-order Rocky Mountain stream. Ninety diatom taxa were identified. *Achnanthes minutissima* Kuetz. and *Navicula lanceolata* (Ag.) Kuetz. dominated the open-canopy site, whereas *Cocconeis placentula* var. *euglypta* (Ehr.) Cl. comprised greater than 40% of the diatom assemblage at the closed-canopy site. Seven of the 10 most important diatoms were present at both sites. A high degree of similarity was evident between natural and artificial substrates at both sites. Although most taxa were present at both sites, it is apparent from this study that differences in the abundance of taxa occur according to variations in light.

The purpose of this paper is threefold: (1) to provide a description of the diatom assemblage present in an open- and a closed-canopy section of a third-order Rocky Mountain stream, (2) to compare our findings with those of other studies on lotic diatom communities from mountain streams in Idaho, and (3) to compare the colonizing diatom assemblage on natural substrates with that on clay brick artificial substrates.

METHODS

Study Area Description

Mink Creek is a third-order stream located in the Caribou National Forest, Bannock County, Idaho, USA (112°23′ W longitude, 42°48′ N latitude). Diatom samples were collected from the East Fork and the main stem. The East Fork site had a closed canopy with solar radiation reaching the stream bed ranging from 80 to 260 uE m^{-2} s^{-1}. The main stem site had an open canopy with solar radiation reaching the stream bed ranging from 310 to 1880 uE m^{-2} s^{-1}. Solar radiation was measured with a Lambda light meter (Model LI–185). Stream temperatures at both sites ranged from 8 to 20 C. Water chemistry was analyzed in the field using a HACH kit. At the time of sampling, pH = 8.9, hardness = 220 mg l^{-1} ($CaCO_3$), ortho-phosphate = 1.0–1.7 mg l^{-1} (PO_4), nitrate = 13–17 mg l^{-1}, and turbidity = 10 FTUs. Additional descriptions of the sites are given by Robinson and Rushforth (1987).

Experimental Methods

Twenty-five half-bricks (4 × 10 × 15 cm) were placed in the stream at each site on 1 July 1983. On 14 November 1983 periphyton was collected in the field by scrubbing a 3.5-cm^2 area from the top of the half-bricks and natural substrates using a technique derived from Stockner and Armstrong (1971). A 35-ml syringe tube was reduced to 5 cm in length by removing the "needle" end, and a neoprene gasket (made from 0.5-cm wet suit material) was glued to the flared "plunger" end. During sampling, the apparatus was pressed onto the substrate surface with the neoprene gasket, thus creating a seal. Periphyton was then scrubbed into a slurry with a coarse brush. This slurry was pipetted into a storage vial, placed on ice, and returned to the laboratory. Two samples were collected from each substrate, one being analyzed for chlorophyll *a* and one for diatoms.

Chlorophyll *a* samples were vacuum filtered (103 kPa) through 2.4-cm Whatman GF/C filters (pore size 0.45 um) and immediately frozen at −20 C for analysis later. Chlorophyll *a* was extracted by grinding the previously frozen filter in 3 ml reagent-grade acetone (100%). The extractant was transferred to a centrifuge tube, filled to 10 ml with acetone, and then refrigerated at 4 C for 24 hours. Chlorophyll *a* and pheaopigment concentrations were determined using a Turner model 111 fluorometer by multiplying the fluorescence reading for each sample by a calibration factor derived with a Beckman Instruments

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TABLE 1. Ten most important diatom taxa, species importance values (FDI), species richness values, and Simpson's diversity values categorized by site and substrate type. N = number of samples. **Species notation descriptions.

Species rating	East bricks N = 25	Main bricks N = 23	All bricks N = 48	East natural N = 5	Main natural N = 2	All combined N = 55
1	COPE	NALA	COPE	COPE	ACMI	COPE
2	NALA	NIDI	NALA	ACMI	NALA	ACMI
3	ACMI	COPE	ACMI	NALA	COPE	NALA
4	ACLA	ACMI	NIDI	NIPA	NACV	NACV
5	AMPE	AMPE	AMPE	GOOL	NIDI	NIDI
6	NIDI	NACV	ACLA	NIDI	NART	NIPA
7	NACV	NATR	NACV	NACV	NATR	GOOL
8	NASA	NASA	NASA	NASA	AMPE	NASA
9	GOOL	ACLA	NIPA	ACLA	NASA	AMPE
10	NIPA	SUOV	GOOL	AMPE	GOOL	ACLA
Importance values						
Top species	48.4	23.2	35.1	42.3	26.9	32.9
Top 5 species	82.9	84.9	81.3	76.6	77.2	75.8
Top 10 species	92.8	91.7	91.3	92.2	90.2	89.7
Others	3.3	5.4	4.9	2.8	7.1	3.2
Species richness	55	79	90	34	40	49
Simpson's diversity	.29	.17	.20	.24	.18	.19

**ACLA *Achnanthes lanceolata* (Brev.) Grun. in Cl. & Grun., ACMI *A. minutissima* Kuetz., AMPE *Amphora perpusilla* (Grun.) Grun., COPE Cocconeis placentula var. *euglypta* (Ehr.) Cl., GOOL *Gomphonema olivaceum* (Lyngb.) Kuetz., NACV *Navicula cryptocephela* var. *veneta* (Kuetz.) Rabh., NALA *N. lanceolata* (Ag.) Kuetz., NART *N. radiosa* var. *tenella* (Breb. ex Kuetz.) Grun., NASA *N. secreta* var. *apiculata* Patr., NATR *N. tripunctata* (D. F. Muell.) Bory, NIDI *Nitzschia dissipata* (Kuetz.) Grun., NIPA *N. paleacea* Grun., SUOV *Surirella ovalis* Breb.

model-DB spectrophotometer (American Public Health Association 1980).

Diatom samples were boiled in concentrated nitric acid, rinsed, and strewn mounts prepared using Naphrax mountant following methods described by St. Clair and Rushforth (1976). The samples were examined under 1,000X oil immersion using a Zeis RA microscope with Nomarski and bright field optics. Each species was photographed for identification. Counts of 300–400 diatom frustules were made from each slide to determine percent relative density, species richness, and Simpson's diversity index (Simpson 1949). The most important diatom taxa present in the study were determined using a species importance index (FDI). This was calculated by multiplying percent presence (frequency) by average percent relative density in all samples (Warner and Harper 1972, Ross and Rushforth 1980, Robinson and Rushforth 1987). Species present on the bricks were added to those from the natural substrates to provide a complete taxonomic listing of the diatoms of Mink Creek.

RESULTS AND DISCUSSION

Chlorophyll *a* values ranged from 30 to 113 g/m^2. The lower chlorophyll values were found at the East Fork site and can be attributed to low light intensity (Towns 1981). Chlorophyll *a* values were found to be highly correlated ($r = .85$) to ash-free dry weights of individual samples. This suggests that chlorophyll values were indicative of algal standing crops in study sections, and that algal material collected was composed primarily of living cells.

The chlorophyll *a* values found in this study were consistent with values found for the Middle Fork of the Salmon River of Idaho (Cushing et al. 1983). Overall, fewer taxa were found in Mink Creek (third order) than in the Middle Fork of the Salmon River (seventh order). In addition, Cushing and Rushforth (1984) found *A. minutissima* Kuetz. and *C. placentula* var. *euglypta* (Ehr.) Cl. to be prevalent in the Middle Fork of the Salmon River. Both of these taxa were predominant in Mink Creek. This predominance of small, adnate growth forms found in Mink Creek can be attributed to grazing by invertebrates (Sumner and McIntire 1982, Gregory 1983, Peterson 1987, Hill and Knight 1988) or frequent physical disturbance (Luttenton and Rada 1986, Robinson and Rushforth 1987).

A total of 90 diatom taxa were identified from Mink Creek. Species richness varied

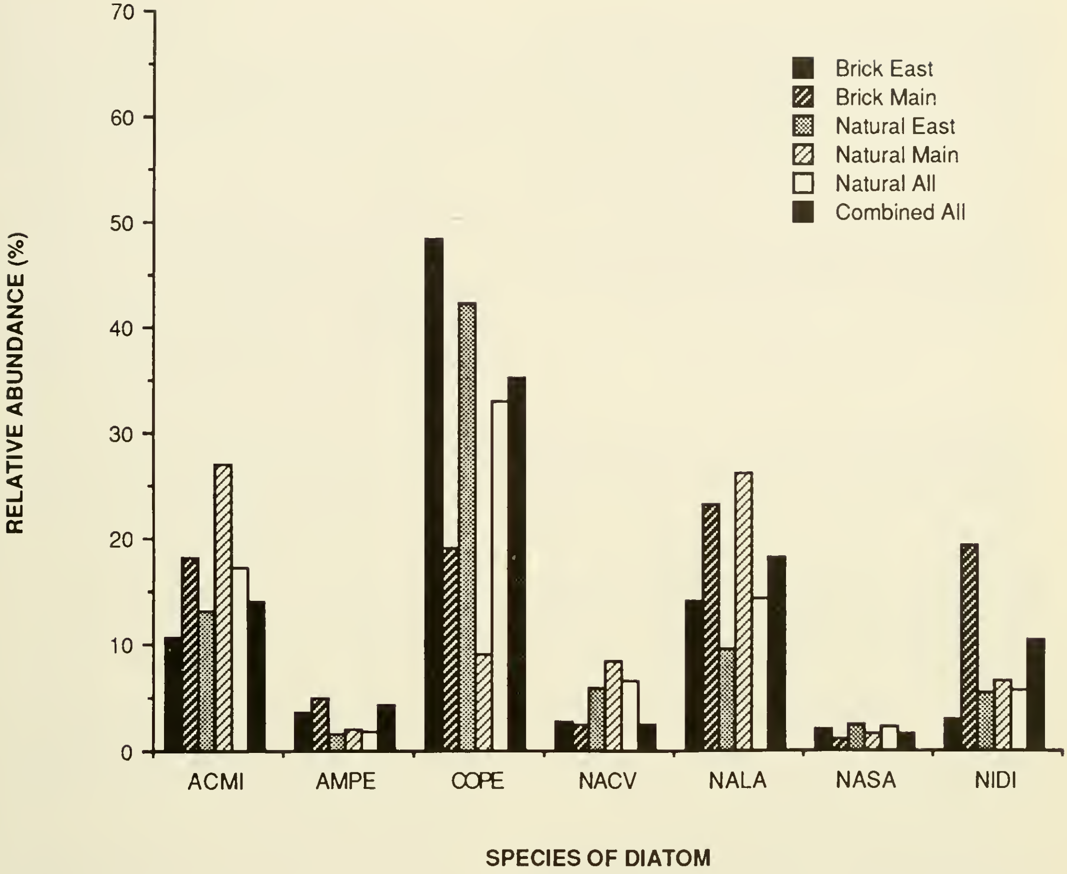

Fig. 1. Relative abundances of 7 diatom taxa from the 10 most important taxa common to each site and substrate type. ACMI = *Achnanthes minutissima* Kuetz., AMPE = *Amphora perpusilla* (Grun.) Grun., COPE = *Cocconeis placentula* var. *euglypta* (Ehr.) Cl., NACV = *Navicula cryptocephela* var. *veneta* (Kuetz.) Rabh., NALA = *Navicula lanceolata* (Ag.) Kuetz., NASA = *Navicula secreta* var. *apiculata* Patr., NIDI = *Nitzschia dissipata* (Kuetz.) Grun.

widely between sites, ranging from 55 taxa at the East Fork to 79 taxa at the main stem (Table 1). Fewer species were found on natural substrates than on the clay half-bricks. The greater number of taxa found on the bricks may simply be an artifact of a difference in sample size (Table 1). The top 10 taxa predominated the system, and 7 of the 10 most important taxa (by FDI) were found in all samples, with the remaining taxa being low in abundance. A complete taxonomic list can be found in Robinson and Rushforth (1987).

Differences also exist within the diatom community between sites. *Cocconeis placentula* var. *euglypta* (Ehr.) Cl. comprised over 40% of the community in the East Fork, whereas *Navicula lanceolata* (Ag.) Kuetz. and *Achnanthes minutissima* Kuetz. dominated the main stem, with combined relative abundances of greater than 53% (Fig. 1). Simpson's index (an index of dominance) was greater in the East Fork than in the main stem (Table 1), further emphasizing the predominance of *C. placentula* var. *euglypta* (Ehr.) Cl. at the East Fork site. Of interest is the evidence of a high degree of similarity among samples within a site, and the relatively low similarity between sites. Considering all samples, the East Fork had an average of 70.1% within-group similarity. The within-group similarity of the main stem equaled 68.2%, whereas between-group similarity equaled only 35%.

Numerous studies have demonstrated good comparability of manufactured substrates with natural substrates after a set colonization period (e.g., Tuchman and Blinn 1979, Tuchman and Stevenson 1980, Lamberti and Resh 1985). Our study also displays good comparability of artificial substrates with natural substrates. However, specific site differences were evident, suggesting that diatom studies should be made at the site-specific scale of study to take into account possible differences in physical or chemical properties between sites (see also Clark and Rushforth 1977).

Acknowledgments

Funding for the project was provided through the Department of Botany and Range Science, Brigham Young University, the Department of Biological Sciences, Idaho State University, and a Sigma Xi Grant-in-Aid of Research. We thank D. M. Anderson, J. R. Barnes, and C. Richards for field and laboratory assistance. We thank G. W. Minshall for reviewing the manuscript.

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RESPONSES OF UTAH DEER HUNTERS TO A CHECKING STATION QUESTIONNAIRE

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Abstract.—During the 1987 deer hunt 4,250 card questionnaires were distributed to Utah hunters at nine checking stations. Return rates varied from a mean 23% when cards were simply handed to hunters, to 50% when hunters' names and telephone numbers were taken. Results concerning methodology suggest that questionnaire surveys conducted from checking stations are efficient and accurate in obtaining hunter opinions. Questionnaire results indicated that most hunters rated the Utah deer hunt as moderately satisfactory, but may prefer alternative options that would result in a higher quality hunt. The majority of hunters indicated that hunter numbers should be limited to current levels or decreased. Unretrieved kill was reported as 21 deer per 100 hunters.

The need to obtain representative opinions concerning mule deer management from Utah hunters is becoming increasingly important to game managers. Recreational impacts upon wildlife populations are expanding, causing a greater need for communication between managers and users. Various vehicles for obtaining hunter input are available, including public meetings, informal meetings with hunting and fishing clubs, direct letters and telephone calls, and public surveys. Since each method has limitations, each should be evaluated and used as appropriate. In this study, hunters were surveyed at established checking stations during the general deer hunt, when opinions about deer hunting were current.

Although most management decisions are based primarily upon biological data, considerable variation in management strategies is available within the boundaries of sound biological practices. Hunter numbers and their effectiveness in harvesting deer in Utah have far exceeded what is necessary to keep deer populations from expanding above range-carrying capacities. Consequently, managers face the question of how best to provide quality hunting to a large hunting public, remove the harvestable surplus, and still obtain adequate license revenues for management needs. The type of hunt (i.e., buck-only vs. either-sex), season length, sex and age structure of harvested deer, and number of hunters participating are areas of management manipulation that can be applied to obtain various levels of hunting quality. These areas of trade-off opportunities need hunter input. This survey addressed some of these issues.

The objectives in this study were to determine (1) feasibility of collecting information from questionnaires handed out at checking stations during the deer hunt, (2) demographics of hunters using checking stations, and (3) hunter information and opinions on several questions related to hunting.

Methods

Questionnaire distribution.—Questionnaires (Appendix A) were printed on 4 × 6 yellow- and red-colored, postage-paid cards. Equal numbers of yellow cards and red cards were distributed, one card to each alternate hunter. On both cards questions 1–10 were identical. The remaining questions differed between cards, with only the responses of the red cards reported in this study. The number of cards given to each of the nine checking stations was proportional to the number of hunters expected at each station. Cards were coded to determine their point of origin. Beginning at 1600 hrs on Sunday, the second day of the deer hunt, every licensed hunter checked at each station was handed a questionnaire and asked to return it as soon as possible. Questionnaires were distributed until the supply was depleted.

At four stations between 1500 and 1600 hrs on Sunday, hunter names and telephone

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TABLE 1. Questionnaire return rates.

Station name	Number of questionnaires distributed	Number returned			% returned
		Red	Yellow	Total	
Snowville	300	44	38	82	27.3
Blacksmith	300	37	30	67	22.3
Ogden	500	47	52	99	19.8
Daniels	719	73	71	144	20.0
Thistle	600	62	63	125	20.8
Sheepcreek	215	30	32	62	28.8
Tucker	200	14	20	34	17.0
Subtotal[1]	2,834	307	306	613	21.6
Bloomington[2]	800	94	91	185	23.1
Vernon[3]	200	42	36	78	39.0
Blacksmith	14	5	4	9	64.3
Ogden	9	2	1	3	33.3
Daniels	50	12	6	18	36.0
Subtotal[4]	73	19	11	30	41.1
Vernon[5]	50	19	13	32	64.0
Daniels[6] (Monday)	100	100	—	100	100.0
Daniels[7] (Monday)	93	21	19	40	43.0
Daniels[1] (Monday)	100	7	12	19	19.0
TOTAL	4,250	609	488	1,097	25.8

[1] Hunters mostly residents from buck-only hunting areas, questionnaires simply handed out.
[2] Hunters mostly nonresidents from buck-only hunting areas, questionnaires simply handed out.
[3] Hunters mostly residents from limited-entry hunting areas, questionnaires simply handed out.
[4] Hunters mostly residents from buck-hunting areas, hunters' names and telephone numbers recorded.
[5] Hunters mostly residents from limited-entry hunting areas, hunters' names and telephone numbers recorded
[6] Hunters mostly residents from buck-only hunting areas, hunters interviewed at checking station
[7] Hunters mostly residents from buck-only hunting areas, hunters' names and telephone numbers recorded.

numbers were recorded before each licensed hunter was handed a questionnaire. This study aspect was designed to determine if return rates could be increased by recording personal information.

Between 1430 and 1600 hrs on Monday, the third day of the deer hunt, personnel at one station randomly selected hunters and interviewed them using the red questionnaire. Between 1600 and 1700 hrs hunter names and telephone numbers were recorded before the hunters received questionnaires. Between 1700 and 1730 hrs additional questionnaires were simply handed to hunters. These variations were designed to compare the consistency in results among three methods of distribution.

Data were analyzed using the chi-square statistic. The cross-tabulation method from the SPSS-X program on the VAX computer was employed. Significance level was set at p = .05 and reported for important interactions.

RESULTS AND DISCUSSION

QUESTIONNAIRE RETURN RATES.—Checking stations used for distribution, the number of questionnaires distributed, and return rates are indicated in Table 1. The Vernon station received mostly hunters from a limited-entry unit, and the Bloomington station checked only nonresident hunters. These two stations may be expected to represent atypical subpopulations of Utah hunters. At the other seven stations a random sample of hunters mostly from buck-only units were given questionnaires.

Rates of return for the seven buck-only stations varied from 17.0 to 28.8%, with a mean of 22.3%. Nonresident hunters (Bloomington station) had a similar return rate (23.1%), while the predominantly resident hunters from the limited-entry area (Vernon station) had a much higher return rate (39.0%). These rates of return are comparable to return rates for big game harvest questionnaires in Utah, which usually range between 25 and 40%, using two mailings. The return rates for this questionnaire are especially encouraging considering its complexity compared with the few, simple questions on harvest questionnaires.

Return rates where hunter names and telephone numbers were recorded were much higher. Mean return rate from the three combined buck-only stations was 41.1% and from the limited-entry station 64.0%. Return rates were approximately doubled by recording names and telephone numbers.

Return rates for questionnaires distributed during the third day of the deer hunt were similar, with 19.0% for surveys simply handed out and 43.0% for surveys on which names and telephone numbers were recorded.

Effect of card color on hunter responses.—The effect of card color was not significant in any of the questions common to both cards. Comparisons made between colors included: (1) combination of all data, (2) type of hunting area, and (3) mode of questionnaire distribution. From the combined seven regular checking stations, return rates of 21.6 and 21.7% for red and yellow cards, respectively, were obtained. Consequently, questions 1–10 from the two card colors were combined.

Effect of distribution mode on hunter responses.—The effect of questionnaire distribution mode on hunter responses was not significant on most questions within checking stations. Only 5 of 70 comparisons were significantly different, and little consistency was found, as only 2 of the 5 significant comparisons represented the same question, suggesting simple random significant differences. We compared data obtained from the relatively small number of hunter interviews (100) and the even smaller number of questionnaires that recorded hunter names and telephone numbers (61). From this comparison we concluded that hunter response to the questionnaire appeared to be unaffected by distribution mode. This result was expected because the same method of random distribution of questionnaires to hunters was used with each mode. Because rates of return were different and hunter responses to the questions were generally not different, nonresponse bias was probably low in this survey. However, two of the significant comparisons concerned the question, "Has a member of your party tagged a deer on this hunt?" Thus, the mode of distribution may have biased hunter response on this question. Nonetheless, data from the different modes were generally insignificant, and data were combined.

Effect of type of hunt on hunter responses.—The effect of type of unit hunted (i.e., buck-only, limited-entry, or 3-point-and-better) had only three significant effects on hunter responses: (1) Hunter participation by sex was affected ($p < .001$); female participation was relatively higher on limited-entry and lower on 3-point-and-better units. (2) Hunter residence was affected ($p < .001$); nonresident participation was proportionately higher on 3-point-and-better areas and lower on limited-entry units. (3) The satisfaction from the 1987 deer hunting experience (question 9, Table 2) was also affected ($p < .05$) in terms of distribution of scores. However, mean scores were not different, with 5.8, 5.8, and 5.9 for limited-entry, 3-point-and-better, and buck-only hunts, respectively. Nonetheless, the limited-entry score may not be representative, as the mean score from the Vernon checking station was 6.9, and included not only the 48 hunters who specified the limited-entry area, but an additional 30 hunters who did not specify the area. More data are needed from limited-entry areas to assess hunter satisfaction. However, the data indicated that restricting hunters to shooting only large deer, 3-point-and-better hunts, had no value in increasing hunter satisfaction.

Effects of checking station on hunter responses.—The effect of checking stations where hunters were mostly residents from buck-only areas produced only five significant differences: (1) Hunter success was significantly different, varying from 29% at the Blacksmith Fork station to 48% at Sheepcreek. (2) Similarly, party success was significantly different, varying from 33% at Blacksmith Fork to 80% at Sheepcreek. (3) Satisfaction with the 1987 deer hunting experience for resident hunters (question 9, Table 2) was also affected, as mean scores ranged from 4.6 at Blacksmith Fork to 6.0 at Daniels Canyon. As may be predicted, higher hunter success was significantly correlated with higher satisfaction scores. It is also important to note that hunter satisfaction for nonresidents (Bloomington station) was higher than for resident hunters, with a value of 6.6. (4) Percentage of hunters with hunting experience on 3-point-and-better units was also significantly different between checking stations, ranging from 43% at Blacksmith Fork to 10% at Thistle. (5) Hunter preferences for the

TABLE 2. Summarized hunter demographics and question responses.

1. Hunter age	16–17	18–24	25–34	35–44	45–54	55–64	65+	Total			
Number (%)	37 (3)	141 (13)	341 (31)	263 (24)	169 (16)	95 (9)	43 (4)	1,089			
2. Hunter sex	Male	Female	Total								
Number (%)	980 (92)	92 (8)	1,070								
3. Hunter residency	Utah	Other	Total								
Number (%)	873 (82)	194 (18)	1,067								
4. Years of Utah deer-hunting experience	1–2	3–5	6–10	11–20	21+	Total					
Number (%)	129 (12)	139 (13)	225 (21)	274 (25)	321 (30)	1,088					
5. Have you tagged a deer on this hunt?	Yes	No	Total								
Number (%)	492 (45)	595 (55)	1,087								
6. Has a member of your party tagged a deer on this hunt?	Yes	No	Total								
Number (%)	672 (62)	405 (38)	1,077								
7. Will you hunt the same unit next year?	Yes	No	Total								
Number (%)	833 (79)	221 (21)	1,054								
8. Did you hunt the same unit last year?	Yes	No	Total								
Number (%)	607 (56)	469 (44)	1,076								
9. 1987 deer-hunting experience compared with past years											
	---------------------			Worst			Best-	-------------------			
Scale	1	2	3	4	5	6	7	8	9	10	Total
Number	71	48	94	78	203	131	122	159	71	116	1,093
(%)	(6)	(4)	(9)	(7)	(19)	(12)	(11)	(15)	(6)	(10)	
10. Have you ever hunted a limited-entry unit?	Yes	No	Total								
Number (%)	109 (18)	484 (82)	593								
11. Have you ever hunted a 3-point-and-better unit?	Yes	No	Total								
Number (%)	125 (21)	475 (79)	600								
12. Hunter preference for number of buck-only units	0	1–55	56	57–73	74	Total					
Number (%)	89 (17)	184 (36)	163 (32)	28 (5)	49 (10)	513					
13. Hunter preference for number of limited-entry units	0	1–7	8	9–73	74	Total					
Number (%)	145 (28)	17 (3)	184 (36)	161 (31)	7 (1)	514					
14. Hunter preference for number of 3-point-and-better units	0	1–9	10	11–73	74	Total					
Number (%)	71 (14)	28 (5)	180 (35)	174 (34)	63 (12)	516					
15. Should hunting pressure and hunting opportunity be reduced?	Yes	No	Total								
Number (%)	364 (62)	222 (38)	586								
16. Should number of hunters be limited to current levels?	Yes	No	Total								
Number (%)	357 (62)	220 (38)	577								
17. Hunter preference for combinations of hunting success and opportunity											
% success	35	45	55	65	75						
Number of hunters	200,000	175,000	156,000	140,000	127,000						
Combination	1	2	3	4	5						
Number	249	85	82	74	73						
(%)	44	15	15	13	13						
18. Did you observe any deer killed and left in the field?	Yes	No	Total								
Number (%)	98 (17)	484 (83)	582								
	(1 deer 84, 2 deer 9, 3+ deer 5)										

hunting success vs. opportunity combinations (question 17, Table 2) were significantly different between stations.

EFFECTS OF HUNTING UNIT ON HUNTER RESPONSES.—Hunting unit effects were highly variable, largely a result of small numbers of hunters (less than 10) surveyed from most of Utah's 74 units. Consequently, the potential effects of hunting unit were not evaluated in this study.

HUNTER DEMOGRAPHICS.—Hunters in this study were mostly 18–55 years of age (84%) with all age groups well represented, male (92%), Utah residents (82%), and highly variable in years of deer hunting experience (Table 2). Krannick and Cundy (1987) and Wasatch Opinion Corporation (1984) reported similar age bracket distribution and sex ratios using completely random designs, suggesting that the sample in this study was representative of the hunting population. Years of deer hunting experience could be divided into four groups of about equal size, those groups being 1–5, 6–10, 11–20, and 21+ years of experience. These data indicate that many hunters quit deer hunting after only a few years of experience. Nonresidents were older ($p < .01$) than residents, had fewer years of experience ($p < .001$), and included a lower proportion of females ($p < .001$). These data suggest that nonresident hunters attracted to Utah are older when they first hunt in Utah and have less hunting experience than Utah residents.

HUNTER SUCCESS RATES.—Forty-five percent of hunters reported tagging a deer in this study, and 62% of the hunting parties were successful in tagging at least one deer. Since hunter response to the questionnaire did not vary between individual vs. party success, this question could be combined on future studies. Surprisingly, neither individual nor party success was related to hunter age, years of hunting experience, or last year's experience on the same unit. This suggests that luck in harvesting a deer, given Utah's high hunter densities, is probably at least as important as age and experience. Because hunting success was not a significant factor in comparing hunter responses for either the number of hunting units preferred by hunters or questions involving hunt quality (questions 12–17, Table 2), but was significant in determining overall hunt satisfaction (question 9), nonresponse bias, as affected by differences in hunter success, was apparently low. It is also interesting to note that success rate for females (57%) was much higher than male success rate (44%) and approached significance ($p = .06$). Illegal use of female licenses by male hunters is one possible explanation.

EXPERIENCE ON HUNTING UNIT.—Hunters planning to return to the same hunting unit the next year had significantly ($p < .001$) higher success rates than hunters not planning to return. Overall, 79% of hunters planned to return to the same unit next year, but only 56% indicated that they hunted the same unit the previous year. These data indicate that almost half of Utah hunters pursue deer in a different area each year. Some interactions were significantly different with respect to unit experience. Nonresidents were less likely than residents to return to the same area ($p < .01$), while older hunters ($p < .05$), and particularly hunters with more deer hunting experience ($p < .001$), were more likely to return to the same areas.

HUNTER SATISFACTION WITH THE UTAH DEER HUNT.—The overall mean satisfaction score was 5.9 on a 10-point scale. This result compares closely to that (5.6) obtained for the 1986 hunt (Krannick and Cundy 1987) and suggests that nonresponse bias in this study was low. As may be expected, successful hunters were more satisfied than unsuccessful hunters ($p < .001$). However, hunter age ($p < .02$) and years of deer hunting experience ($p < .01$) were also significant interactions. Older hunters and those with more experience were less satisfied than younger hunters. One explanation is that success rate and size of bucks harvested have decreased during the last 15 years (Austin et al. 1989) and may have diminished the perceived quality of the experience.

EFFECT OF HUNTING EXPERIENCE ON LIMITED-ENTRY AND 3-POINT-AND-BETTER UNITS ON HUNTER RESPONSES.—Overall, 18 and 21% of hunters indicated previous experience on limited-entry and 3-point-and-better units, respectively. Hunters with experience in one of these types of hunts also tended to have experience in the other ($p > .001$). Also, hunters with 6–10 years of experience and mostly in the 25–34-year-old age bracket had a much higher rate of participation in 3-point-and-better units ($p < .001$), but not on limited-entry hunts.

HUNTER PREFERENCE FOR NUMBER OF BUCK-ONLY, LIMITED-ENTRY, AND 3-POINT-AND-BETTER UNITS.—This open-ended question yielded medians for number of preferred units of 50, 8, and 10 for buck-only, limited-entry, and 3-point-and-better units, respectively, which corresponded closely to the current number of designated units, 56, 8, and 10, respectively. Hunters with experience on 3-point-and-better units preferred fewer buck-only units ($p < .03$) and more 3-point-and-better units ($p < .001$) than did hunters without experience. Hunters with experience on limited-entry units preferred more limited-entry units ($p < .03$) than did hunters without experience, but about the same number of buck-only hunts.

HUNTER PREFERENCES FOR QUALITY HUNTING.—The majority of hunters indicated they would prefer (1) reducing hunting pressure and opportunity, and thus harvesting a higher proportion of mature deer ($p < .001$), and (2) limiting hunter numbers to current levels ($p < .001$) (questions 15, 16, Table 2). A minority of hunters (41%) indicated they would prefer that hunter numbers be substantially reduced below current levels, while the majority (59%) preferred little or no change in hunter numbers (question 17, Table 2). Combined, these three questions indicated that most hunters are satisfied with the current level of hunter participation but strongly prefer that the number of hunters be restricted to current levels (license sales about 200,000). Furthermore, the size of harvested bucks was important to hunters, as they indicated a willingness to decrease hunting opportunity in order to have a higher proportion of mature bucks in the harvest. Similar results were found by Wasatch Opinion Corporation (1984).

Importantly, hunter success was unrelated to responses regarding hunting quality: unsuccessful as well as successful hunters were in agreement on preference for improved quality. Also, the question (#16) dealing with limiting hunter numbers to current levels was unrelated to hunting satisfaction scores, again indicating that hunters are united in this area. Similar conclusions were reported by Krannick and Cundy (1987).

Generally, hunters with experience on limited-entry and 3-point-and-better units were in stronger support for higher quality ($p < .05$) than were hunters without experience. Interactions among the three quality questions indicated hunters were consistent in quality preferences ($p < .001$).

UNRETRIEVED DEER.—The number of deer reported killed and left in the field, which included both illegal kill and crippling loss, was very high, with 20.6 deer reported/100 hunters (5.1 bucks, 11.2 does, 4.3 fawns, and 1.0 unclassified). The number of unretrieved deer reported/100 legal bucks checked was 47.2 (11.7 bucks, 23.4 does, 9.8 fawns, and 2.3 unclassified).

Robinette et al. (1977) stated that hunters reported 2.4–16.3 (mean = 7.6) unretrieved deer/100 hunters on the Oak Creek deer unit between 1948 and 1959 under either-sex hunts. Unpublished data (1980–82) from the Vernon deer unit under heavy, buck-only hunting pressure indicated 1.3–2.5 (mean = 2.0) discrete unretrieved deer/100 hunters or a mean of 17.5 unretrieved deer/100 legal bucks checked. Stapley (1970) reported 26.3 unretrieved deer/100 legally harvested bucks on buck-only units and 8.5 under either-sex hunting. Using his figures, we calculated that unretrieved deer increased 311% when hunts were shifted from either-sex to buck-only. Losch and Samuel (1976) summarized existing data and obtained a mean percent increase of 270%.

In Utah during 13 years (1961–73) of regular season, either-sex hunting, a total mean from all hunts of 37,796 antlerless deer and 64,719 bucks were harvested annually. During 13 years of regular season, buck-only hunts (1974–86), 63,339 bucks were harvested annually, but only 6,088 antlerless deer. Because differences in buck harvest (−2.1%), number of hunters (+6.8%), and full recruitment rate (+3.4%) showed only minor changes between periods, we would expect differences in the total deer population to be small. Although other factors, such as weather, may have differed between the two periods, the increase in unretrieved deer during the regular hunt may account for at least part of the difference in the antlerless harvest. The ratio of the difference in antlerless harvest between the two periods (31,709) to the annual legal buck harvest (1974–86) is calculated at .501. Thus, an estimate of 50.1 unretrieved deer/100 legal deer harvested can be projected. This figure is close to the 47.2 unretrieved deer/100 legal harvested as determined in this study, and it is considerably higher than figures reported for either-sex hunts (Losch and Samuel 1976, Robinette et al. 1977, Stapley 1970).

No significant relationships were found with hunter demographics, success, or experience on types of hunting units. Apparently, all hunters were equally likely to find unretrieved deer. However, it was surprising that the number of unretrieved deer was not significantly different among the three types of hunting units. Hunters reported 36, 25, and 20 unretrieved deer/100 hunters from limited-entry, 3-point-and-better, and buck-only units, respectively, with 8, 10, and 5 unretrieved bucks, respectively. Data suggest that increased sample sizes would increase levels of significance. Additional information should be collected concerning types of hunting units, potential differences between vegetative types, and length (1–11 days) of the hunt.

Conclusions

Distribution of hunter questionnaires at established checking stations in Utah appears to be a time-saving and economic approach for obtaining hunter opinions. Return rates in the 20–30% range would be expected and would yield demographic and hunter opinion information representative of the hunting population.

Hunter response from this study indicated the following conclusions:

1. Mean age of Utah hunters was 35–44 years, and mean number of years of deer hunting experience was 11–20 years.
2. No difference was found between the three types of hunts, buck-only, limited-entry, 3-point-and-better, during the regular season with respect to hunter satisfaction.
3. Hunters were generally in agreement with the number of each type of hunt as currently managed.
4. Hunter age, years of experience, and hunting area familiarity were not related to success, and almost half of Utah deer hunters selected a different unit to hunt between years.
5. Hunters indicated a strong and consistent desire to improve the quality of the deer hunt in terms of possibly reducing number of hunters, increasing the quality of harvested bucks, and, particularly, limiting number of hunters to the current level.
6. The numbers of deer that were killed and not retrieved were substantial, equal to about 47% of the number of legally harvested bucks, and were consistently high regardless of hunt type or area.

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APPENDIX A.

Dear Hunters: In order to manage deer better for Utah hunters, we are asking for your opinions about deer hunting in Utah. Please answer the following questions and mail the questionnaire on your trip home. (No postage required.)

1. Age: 16–17 18–24 25–34 35–44 45–54 55–64 65+
2. Sex: MALE FEMALE
3. Residence: UTAH OTHER
4. Years of deer-hunting experience in Utah:
   1–2 3–5 6–10 11–20 21+
5. Have you tagged a deer on this hunt? YES NO
6. Has a member of your party tagged a deer on this hunt? YES NO
7. Which Utah deer unit did you hunt? ____________
8. Do you anticipate hunting this unit next year? YES NO
9. Did you hunt this unit last year? YES NO
10. Using a scale of 1 to 10, where 1 means that your deer-hunting experience was the worst ever, and 10 means that your experience was the best ever, circle the number which best describes your deer-hunting experience this year.
    1 2 3 4 5 6 7 8 9 10
11. Have you ever hunted on a limited-entry unit? YES NO
12. Have you ever hunted on a 3-point-and-better unit? YES NO
13. Utah has 74 deer management units. They are managed as regular buck hunts, limited-entry hunts, or 3-point-and-better hunts. Please write in how many of each type of hunt you would prefer.

Type of Unit	Current Number of Units	Your Preference
Regular buck hunts	56	______
Limited-entry hunts	8	______
3-point-and-better hunts	10	______
Total	74	74

14. On regular buck hunts, hunter pressure is high and about 25% of the bucks harvested are mature (3-point and better). By reducing hunter pressure, which means hunting opportunity would also be reduced, the percent of mature bucks in the harvest would increase. Circle your choice of the alternatives below.
    A. DO NOT REDUCE HUNTING PRESSURE
    B. REDUCE HUNTING PRESSURE AND INCREASE HARVEST PERCENT OF MATURE BUCKS
15. Right now, Utah has about 200,000 deer hunters. In the next few years the number of people wishing to hunt could increase. If hunter numbers increase, circle your choice of the alternatives below.
    A. DO NOT LIMIT HUNTER NUMBERS
    B. LIMIT NUMBER OF HUNTERS TO CURRENT LEVEL BY RESTRICTING PERMITS
16. Utah hunters harvest about 70,000 bucks each year with a 35% success rate. One way to increase success rate is to reduce the number of hunters. Below are some combinations of success rate, how often the average hunter could expect to draw a permit if number of hunters were restricted, and number of Utah hunters. Circle the combination below you would prefer.

Combination	Success Rate	% Chance Average Hunter Draws Permit	Number of Utah Hunters
1	35	100	200,000
2	40	88	175,000
3	45	78	156,000
4	50	70	140,000
5	55	64	127,000

17. Did you observe any deer killed and left in the field?
    YES NO Sex: M or F Age: FAWN or ADULT

NOMENCLATURAL CHANGES AND NEW SPECIES OF SCOLYTIDAE (COLEOPTERA), PART IV

Stephen L. Wood[1]

ABSTRACT.— Presented from a worldwide treatment of the Scolytidae are cases of new synonymy, replacement names for newly detected junior homonyms, and the descriptions of species new to science as follows. New synonymy includes: *Acanthotomicus quadrituberculatus* (Schedl) (=*Mimips fallax* Eggers), *Amasa schlichi* (Stebbing) (=*Xyleborus glaber* Eggers, *Xyleborus brevipennis* Schedl), *Ambrosiodmus apicalus* (Blandford) (=*Xyleborus cristatus* Hagedorn, *Xyleborus fabricii* Schedl), *Ambrosiodmus asperatus* (Blandford) (=*Xyleborus citri* Beeson, *Xyleborus cristatuloides* Schedl), *Ambrosiodmus colossus* (Blandford) (=*Xyleborus szentivanyi* Schedl), *Ambrosiodmus declivispinatus* (Schedl) (=*Xyleborus tectus* Schedl), *Ambrosiodmus funereus* (Lea) (=*Xyleborus nepos robustus* Schedl), *Ambrosiodmus hagedorni* (Iglesias) (=*Ambrosiodmus guatemalensis* Hopkins), *Ambrosiodmus lewisi* (Blandford) (=*Xyleborus lewekianus* Eggers), *Ambrosiodmus obliquecaudata* (Motschulsky) (=*Xyleborus semirufus* Schedl), *Ambrosiodmus obliquus* (LeConte) (=*Xyleborus melanarius* Schedl), *Ambrosiodmus rubricollis* (Eichhoff) (=*Xyleborus taboensis* Schedl, *Xyleborus strohmeyeri* Schedl), *Arixyleborus canaliculatus* (Eggers) (=*Arixyleborus subsimilis* Schedl), *Arixyleborus imitator* (Eggers) (=*Xyleborus granistriatus* Eggers), *Arixyleborus leprosulus* Schedl (=*Arixyleborus aralidii* Nunberg), *Arixyleborus mediosectus* (Eggers) (=*Xyleboricus angulatus* Schedl), *Camptocerus major* (Eggers) (=*Camptocerus uniseriatus* Schedl), *Camptocerus orientalis* Eggers (=*Camptocerus tectus* Eggers), *Camptocerus suturalis* (Fabricius) (=*Camptocerus hirtipennis* Schedl), *Coccotrypes advena* Blandford (=*Dendrurgus philippinensis* Eggers, *Dendrurgus ternatensis* Eggers, *Dendrurgus minor* Eggers, *Thamnurgides tutuilensis* Beeson), *Coccotrypes barbatus* (Schedl) (=*Thamnurgides ater* Eggers, *Thamnurgides dipterocarpi* Beeson, *Thamnurgides bambusae* Beeson), *Coccotrypes carpophagus* (Hornung) (=*Coccotrypes trevori* Beeson, *Coccotrypes pilosulus* Schedl, *Coccotrypes ceylonicus* Schedl, *Coccotrypes grisseopuberulus* Schedl, *Coccotrypes exasperatus* Schedl), *Coccotrypes cyperi* (Beeson) (=*Poecilips subaplanatus* Schedl), *Coccotrypes dactyliperda* (Fabricius) (=*Coccotrypes borassi* Beeson, *Coccotrypes eleocarpi* Beeson), *Coccotrypes longior* (Eggers) (=*Poecilips oblongus* Eggers, *Poecilips nitidipennis* Schedl, *Poecilips apicatus* Schedl), *Coccotrypes myristicae* (Roepke) (=*Thamnurgides masoni* Beeson), *Coccotrypes nitidus* Eggers (=*Poecilips aterrimus* Schedl), *Coccotrypes nubilus* Blandford (=*Thamnurgides parvus* Beeson, *Thamnurgides himalayensis* Beeson, *Thamnurgides corticus* Beeson, *Thamnurgides brevipilosus* Beeson, *Poecilips mauritianus* Browne), *Coccotrypes papuanus* (Eggers) (=*Thamnurgides rubidus* Beeson), *Coccotrypes rhizophorae* (Hopkins) (=*Thamnurgides shanorum* Beeson), *Coccotrypes salakensis* (Schedl) (=*Thamnurgides opacifrons* Beeson, *Poecilips acuminatus* Schedl), *Conophthorus edulis* Hopkins (=*Conophthorus cembroides* Wood), *Conophthorus resinosae* Hopkins (=*Conophthorus banksianae* McPherson), *Coptoborus usagaricus* (Eggers) (=*Xyleborus usagaricus subadjunctus* Schedl, *Streptocranus hendrickxi* Schedl, *Xyleborus monticolus* Schedl, *Xyleborus fallaciosus* Schedl), *Coptodryas elegans* (Sampson) (=*Xyleborus concinnus* Beeson), *Coptodryas myristicae* (Schedl) (=*Xyleborus theae* Eggers, *Xyleborus brevipilosus* Eggers, *Xyleborus cylindripennis* Schedl), *Coptodryas nugax* (Schedl) (=*Xyleborus fragosus* Schedl), *Coptodryas recidens* (Sampson) (=*Xyleborus minutissimus* Eggers), *Coptodryas undulatus* (Sampson) (=*Xyleborus leprosulus* Schedl), *Cryphalus major* Stebbing (=*Cryphalus morinda* Stebbing), *Cryphalus ruficollis* Hopkins (=*Cryphalus fraseri* Hopkins), *Cryphalus scabricollis* Eichhoff (=*Cryphalus discretus* Eichhoff, *Cryphalus dilutus* Eichhoff), *Cryphalus sylvicola* (Perkins) (=*Cryphalus swezeyi* Schedl, *Cryphalus sylvicola obliquus* Schedl), *Crypturgus pusillus* (Gyllenhal) (=*Crypturgus minimus* Eggers), *Cyrtogenius luteus* (Blandford) (=*Carposinus pini* Hopkins), *Dryocoetes autographus* (Ratzeburg) (=*Dryocoetes brasiliensis* Schedl), *Dryocoetiops laevis* (Strohmeyer) (=*Poecilips loebli* Schedl), *Dryocoetoides paradoxus* (Schedl) (=*Xyleborus solitaripennis* Schedl), *Dryocoetoides pseudosolitarius* (Eggers) (=*Xyleborus pseudosolitarius schizolobius* Schedl), *Eccoptopterus gracilipes* (Eichhoff) (=*Xyleborus collaris* Eggers), *Eccoptopterus limbus* Sampson (=*Xyleborus squamulatus duplicatus* Eggers), *Eidophelus imitans* Eichhoff (=*Phellodendrophagus elegans* Krivolutskaya, *Ptilopodius nitidus* Schedl), *Ernocladius corpulentus* (Sampson) (=*Margadillius corpulentus sundri* Schedl), *Ernoporus antennarius* Schedl (=*Euptilius papuanus* Browne), *Euwallacea andamanensis* (Blandford) (=*Xyleborus granulipennis* Eggers, *Xyleborus intextus* Beeson, *Xyleborus senachalensis* Beeson), *Euwallacea bicolor* (Blandford) (=*Xyleborus bicolor unimodus* Beeson, *Xyleborus rodgeri* Beeson, *Xyleborus rodgeri privatus* Beeson), *Euwallacea destruens* (Blandford) (=*Xyleborus pseudobarbatus* Schedl, *Xyleborus nandarivatus* Schedl), *Euwallacea fornicatus* (Eichhoff) (=*Xyleborus whitfordiodendrus* Schedl, *Xyleborus perbrevis* Schedl, *Xyleborus schultzei* Schedl, *Xyleborus tapatapaoensis* Schedl), *Euwallacea quadraticollis* (Eggers) (=*Xyleborus duplicatus* Schedl), *Euwallacea sibsagaricus* (Eggers) (=*Xyleborus dalbergiae* Eggers), *Euwallacea velatus* (Sampson) (=*Xyleborus assamensis* Eggers, *Xyleborus asperipennis* Eggers), *Euwallacea wallacei* (Blandford) (=*Xyleborus siporanus* Hagedorn, *Xyleborus ovalicollis* Eggers, *Xyleborus perakensis* Schedl), *Euwallacea xanthopus* (Eichhoff) (=*Xyleborus semirudis* Blandford,

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Xyleborus rudis Eggers, *Xyleborus semipilosus* Eggers, *Xyleborus neohybridus* Schedl, *Xyleborus artehybridus* Schedl), *Gnathotrupes bituberculatus* (Blandford) (= *Gnathotrichus impressus* Schedl), *Gnathotrupes longipennis* (Blanchard) (= *Gnathotrichus obnixus* Schedl, *Gnathotrichus corthyloides* Schedl, *Gnathotrichus corthyliformis* Schedl, *Gnathotrupes constrictus* Schedl), *Gymnochilus consocius* (Blandford) (= *Problechilus novateutonicus* Schedl), *Hypocryphalus mangiferae* (Stebbing) (= *Hypocryphalus opacus* Schedl), *Hypocryphalus sandakanensis* (Schedl) (= *Hypocryphalus maculatus* Browne), *Hypothenemus areccae* (Hornung) (= *Stephanoderes bambesanus* Eggers, *Hypothenemus bauhaniae* Schedl, *Stephanoderes occidentalis* Schedl), *Hypothenemus birmanus* Eichhoff (= *Stephanoderes nibarani* Beeson, *Stephanoderes ampliatus* Eggers), *Hypothenemus californicus* Hopkins (= *Stephanoderes zeae* Schedl), *Hypothenemus crudiae* (Panzer) (= *Cryphalus mucronifer* Wollaston), *Hypothenemus donisi* (Schedl) (= *Ericryphalus madagascarensis* Schedl), *Hypothenemus eruditus* Westwood (= *Cryphalus tectonae* Stebbing, *Cryphalus striatopunctatus* Lea, *Cryphalus tantillus* Lea, *Hypothenemus tuberculatus* Hagedorn, *Hypothenemus pusillus* Eggers, *Hypothenemus argentinensis* Schedl, *Hypothenemus cylindricus* Schedl, *Hypothenemus asaroriensis* Beeson, *Hypothenemus mauiensis* Schedl, *Stephanoderes nanulus* Schedl, *Hypothenemus parilis* Schedl, *Hypothenemus obscuripes* Schedl, *Stephanoderes tigrensis* Schedl, *Hypothenemus parcius* Schedl, *Hypothenemus cylindripennis* Schedl, *Hypothenemus vianai* Schedl, *Hypothenemus mesoleius* Schedl, *Hypothenemus minutulus* Schedl, *Cryphalus minutus* Schedl), *Hypothenemus fuscicollis* (Eichhoff) (=*Stephanoderes sundaensis* Eggers, *Hypothenemus ghanaensis* Schedl), *Hypothenemus hampei* (Ferrari) (= *Stephanoderes glabellus* Schedl), *Hypothenemus ingens* (Schedl) (=*Cryphalomorphus grandis* Schedl), *Hypothenemus plumeriae* (Nördlinger) (=*Stephanoderes cylindricus* Hopkins, *Hypothenemus guadeloupensis* Schedl, *Stephanoderes ituriensis* Schedl), *Hypothenemus pubescens* Hopkins (=*Hypothenemus minutissimus* Schedl), *Hypothenemus seriatus* (Eichhoff) (= *Cryphalus aulmanni* Hagedorn, *Hypothenemus cassavaensis* Schedl, *Stephanoderes hawaiiensis* Schedl, *Hypothenemus striatulus* Schedl, *Hypothenemus marovoayi* Schedl, *Hypothenemus asperatus* Schedl), *Hypothenemus stigmosus* (Schedl) (=*Stephanoderes garciae* Schedl), *Leptoxyleborus concisus* (Blandford) (=*Xyleborus incurvus* Eggers), *Leptoxyleborus depressus* (Eggers) (=*Xyleborus sejugatus* Schedl), *Leptoxyleborus semigranulatus* (Schedl) (=*Xyleborus artemarginatus* Schedl), *Monarthrum chapuisi* Kirsch (=*Monarthrum bolivianum* Eggers), *Monarthrum ingens* (Eichhoff) (=*Pterocyclon assequens* Schedl), *Pityophthorus deodara* (Stebbing) (=*Cryphalus himalayensis* Stebbing, *Pityophthorus sampsoni* Stebbing), *Sauroptilius sauropterus* (Schedl) (=*Xyleborus sauropteroides* Schedl), *Scolytogenes knabi* (Hopkins) (=*Cryphalomorphus alienus* Schedl), *Scolytomimus pusillus* (Eggers) (=*Scolytomimus kalshoveni* Schedl, *Scolytocleptes insularis* Schedl), *Scolytoplatypus mikado* Blandford (= *Scolytoplatypus sinensis* Tsai & Huang), *Scolytoplatypus papuanus* Eggers (=*Scolytoplatypus luzonicus* Eggers), *Scolytoplatypus siomio* Blandford (=*Scolytoplatypus kunala* Strohmeyer), *Scolytopsis puncticollis* Blandford (=*Scolytopsis cubensis* Wood), *Terminalinus crucipennis* (Schedl) (=*Xyleborus metacrucifer* Browne), *Terminalinus hirtus* (Hagedorn) (=*Xyleborus hirtuosus* Beeson), *Trypodendron laeve* Eggers (=*Trypodendron piceum* Strand), *Theoborus ricini* (Eggers) (=*Xyleborus solitariceps* Schedl), *Webbia quattuordecimspinatus* or *14-spinatus* Sampson (= *Webbia quattuordecimspinatus* or *14-spinatus* Schedl), *Xyleborinus andrewesi* (Blandford) (=*Xyleborus persphenos* Schedl), *Xyleborinus artestriatus* (Eichhoff) (=*Xyleborus rugipennis* Schedl), *Xyleborinus gracilis* (Eichhoff) (=*Xyleborus neogracilis* Schedl), *Xyleborinus saxeseni* (Ratzeburg) (=*Xyleborus subspinosus* Eggers, *Xyleborus pseudogracilis* Schedl, *Xyleborus retrusus* Schedl, *Xyleborus paraguayensis* Schedl, *Xyleborus cinctipennis* Schedl), *Xyleborus adelographus* Eichhoff (=*Xyleborus accomodatus* Schedl), *Xyleborus adusticollis* (Motschulsky) (=*Xyleborus vestitus* Schedl), *Xyleborus approximatus* Schedl (=*Xyleborus potens* Schedl), *Xyleborus biconicus* Eggers (=*Xyleborus bicinctus* Schedl), *Xyleborus bidentatus* (Motschulsky) (=*Xyleborus quadridens* Eggers), *Xyleborus caraibicus* Eggers (=*Xyleborus variabilis* Schedl), *Xyleborus crinitus* Schedl (=*Xyleborus nigericus* Browne), *Xyleborus emarginatus* Eichhoff (=*Xyleborus emarginatus semicircularis* Schedl), *Xyleborus eximius* Schedl (=*Xyleborus apicenotatus* Schedl), *Xyleborus fallax* Eichhoff (=*Xyleborus amphicranulus* Eggers), *Xyleborus ferrugineus* (Fabricius) (=*Xyleborus rufopiceus* Eggers), *Xyleborus grossmanni* Schedl (=*Xyleborus acuminatus* Schedl), *Xyleborus mascareniformis* Eggers (=*Xyleborus onerosus* Schedl), *Xyleborus multispinatus* Eggers (=*Xyleborus acanthus* Schedl), *Xyleborus mutabilis* Schedl (=*Xyleborus itatiayaensis* Schedl), *Xyleborus perforans* (Wollaston) (=*Xyleborus criticus* Schedl), *Xyleborus perlongus* Eggers (=*Xyleborus pulcherrimus* Schedl, *Xyleborus pulcheripes* Schedl), *Xyleborus similis* Ferrari (=*Xyleborus novaguineanus* Schedl, *Xyleborus dilatatulus* Schedl), *Xyleborus subcostatus* Eichhoff (=*Xyleborus subcostatus dearmatus* Eggers), *Xyleborus sulcicauda* Schedl (=*Xyleborus tenuipennis* Browne), *Xyleborus volvulus* (Fabricius) (=*Xyleborus silvestris* Beeson, *Xyleborus granularis* Schedl), *Xylosandrus ater* (Eggers) (=*Xyleborus retusiformis* Schedl), *Xylosandrus cylindrotomicus* (Schedl) (=*Xyleborus semitruncatus* Schedl, *Xyleborus ramulorum* Schedl), *Xylosandrus mutilatus* (Blandford) (=*Xyleborus sampsoni* Eggers). The species *Cosmocorynus vagabundus* Schedl is transferred to the genus *Amphicranus*, and the species *Xyleborus lineatopunctatus* Eggers is transferred to the genus *Cyrtogenius*. New names are proposed for junior homonyms as follows: *Araptus frontis* (for *Gnathocranus frontalis* Schedl 1978, now in *Araptus*), *Araptus guadeloupanus* (for *Brachydendrulus guadeloupensis* Schedl 1970, now in *Araptus*), *Coccotrypes brunnipes* (for *Coccotrypes brunneus* Nunberg 1973), *Coccotrypes robustulus* for *Poecilips robustus* Schedl 1972, now in *Coccotrypes*), *Coccotrypes striatulus* (for *Thamnurgides striatus* Eggers 1927, now in *Coccotrypes*), *Hypothenemus aterrimulus* (for *Lepiceroides aterrimus* Schedl 1957, now in *Hypothenemus*), *Hypothenemus ruginosus* (for *Pachynoderes rugifer* Schedl 1977, now in *Hypothenemus*), *Mimiocurus monticulus* (for *Mimiocurus montanus* Schedl 1957), *Monarthrum boliviensis* (for *Cosmocorynus bolivianus* Schedl 1970, now in *Monarthrum*), *Monarthrum dentatulum* (for *Monarthrum dentatum* Eggers 1935), *Monarthrum sexdenticulum* (for *Anchonocerus sexdentatus* Eggers 1935, now in *Monarthrum*), *Pityophthorus abietinus* (for *Pityophthorus abietis* Kurenzov 1941 and *P. sibericus* Nunberg 1956), *Pityophthorus brighti* (for *Pityophthorus blackmani* Bright 1977), *Pityophthorus micrograptinus* (for *Breviophthorus micrographus* Schedl 1972, now in *Pityophthorus*), *Pityophthorus subsimilans* (for *Breviophthorus subsimilis* Schedl 1966, now in *Pityophthorus*),

Scolytogenes papuensis (For *Xylocryptus papuanus* Schedl 1975, now in *Scolytogenes*. The following names are described as new to science: *Cryphalus dipterocarpi* (India), *Cryphalus felis* (India), *Cryphalus fulmineus* (India), *Gnathotrupes colaphus* (Venezuela), *Gnathotrupes nectandrae* (Venezuela), *Mimiocurus beesoni* (India), *Pityophthorus cedri* (India), *Pityophthorus chilgoza* (India), *Pityophthorus glutae* (India), and *Scolytogenes indicus* (India).

During the compilation of a world catalog of Scolytidae and Platypodidae (Part 1, the bibliography, published as Wood and Bright 1987), a number of taxonomic errors, omissions, and discrepancies were encountered that require validation or correction before the taxonomic portion of the catalog is published. This article is written for the purpose of attending to those taxonomic housekeeping chores. Included are 214 cases of new or previously unconfirmed synonymy, 16 new names proposed as replacements for junior homonyms, 2 species transferred from the genus where each was originally named to the genus where each properly belongs in current classification, and 10 species (8 from India, 2 from Venezuela) named as new to science.

NEW SYNONYMY

Listed below is new synonymy of species from all areas of the world. The synonymy was discovered in recent visits to museums, the most notable visits being made by me to (1) the Institute of Zoology, Academy of Science, Moscow, in 1968 to study the Motschulsky types from Sri Lanka and India; (2) the Forest Research Institute (hereafter FRI), Dehra Dun, India, in 1981 to study types named by Stebbing, Beeson, and Eggers from India and neighboring areas; (3) the Naturhistorische Museum Wien, in 1983 to study types named by Schedl and Ferrari; and (4) the British Museum (Natural History) in 1981 to study the types of species named by Browne, etc. A few additional types were received through loans from various other institutions. Each species is listed in alphabetical order under the senior name with its author and year and page of original validation of that name. If the specific name has been transferred to the current genus, the original genus is indicated. Next, the kind of type or other specimen on which the synonymy was based is indicated; and following this, in parentheses, is the original combination of the new synonym, with its author and year and page of validation, and the kind of type or other specimens on which the synonymy is based. Unless otherwise noted, the direct comparisons were made by me or direct comparisons were made to my specimens, which were then compared directly to the synonym. While many of the synonymies are not based on the primary type of one or both members, the identifications are deemed sufficiently authentic to list along with a recommendation to future workers to confirm these observations with additional study. For complete references to the literature cited by the author, names, and validation dates, see S. L. Wood and D. E. Bright (1987). The treatment of genera is based on S. L. Wood (1986).

Acantotomicus quadrituberculatus (Schedl 1938:173), originally in *Isophthorus*, holotype in Wien Museum compared to (=*Mimips fallax* Eggers 1943:76) paratype in Wien Museum.

Amasa schlichi (Stebbing 1914:592), originally in *Xyleborus*, FRI syntypes compared to (=*Xyleborus glaber* Eggers 1930:387) holotype at FRI, also compared to (=*Xyleborus brevipennis* Schedl 1971:387) my homotypes, holotype also examined.

Ambrosiodmus apicalis (Blandford 1894: 105), originally in *Xyleborus*, my homotypes, holotype examined, compared to (=*Xyleborus cristatus* Hagedorn 1908:377 and its replacement *Xyleborus fabricii* Schedl 1964: 217) Schedl homotypes in Wien Museum.

Ambrosiodmus asperatus (Blandford 1895: 321), originally in *Xyleborus*, my homotypes, holotype examined, compared to (=*Xyleborus citri* Beeson 1930:215) FRI syntypes, also (=*Xyleborus cristatuloides* Schedl 1971: 284) Schedl paratype in Wien Museum.

Ambrosiodmus colossus (Blandford 1896: 207), originally in *Xyleborus*, female determined by Schedl in Wien Museum compared to (=*Xyleborus szentivanyi* Schedl 1968:267) holotype in Wien Museum.

Ambrosiodmus declivispinatus (Schedl 1970: 216), originally in *Xyleborus*, Schedl paratypes in Wien Museum compared to (=*Xyleborus tectus* Schedl 1972:63) Schedl paratype in Wien Museum.

Ambrosiodmus funereus (Lea 1910:139), originally in *Xyleborus*, Schedl specimens in Wien Museum compared to (=*Xyleborus* *nepos robustus* Schedl 1933:103) Schedl syntypes in Wien Museum.

Ambrosiodmus hagedorni (Iglesias 1914: 128), originally in *Xyleborus*, Schedl paratypes in Wien Museum compared to (=*Ambrosiodmus guatemalensis* Hopkins 1915:56) my homotypes, holotype in U.S. National Museum examined.

Ambrosiodmus lewisi (Blandford 1894:104), originally in *Xyleborus*, my homotypes, syntypes in British Museum (Natural History) examined, compared to (=*Xyleborus lewekianus* Eggers 1923:181) Beeson and Eggers homotypes in FRI.

Ambrosiodmus obliquecaudata (Motschulsky 1863:513), originally in *Phloeotrogus*, my homotypes, syntypes examined, compared to (=*Xyleborus semirufus* Schedl 1959:499) paratype in Wien Museum, holotype examined.

Ambrosiodmus obliquus (LeConte 1878: 432), originally in *Pityophthorus*, my homotypes, holotype examined, compared to (=*Xyleborus melanarius* Schedl 1978:307) holotype in Wien Museum.

Ambrosiodmus rubricollis (Eichhoff 1875: 202), originally in *Xyleborus*, my homotypes, holotype examined, compared to (=*Xyleborus taboensis* Schedl 1952:65) holotype in Wien Museum, also compared to (=*Xyleborus strohmeyeri* Schedl 1975:457) holotype in Wien Museum.

Amphicranus vagabundus (Schedl 1966: 124), holotype examined, the species is here transferred from the original genus *Cosmocorynus* to *Amphicranus*.

Arixyleborus canaliculatus (Eggers 1923: 216), originally in *Xyleboricus*, my homotypes, holotype examined, compared to (=*Arixyleborus subsimilis* Schedl 1970:362) Schedl paratypes in Wien Museum.

Arixyleborus imitator (Eggers 1927:105), originally in *Webbia*, my homotypes, holotype examined, compared to (=*Xyleborus granistriatus* Eggers 1940:147) holotype in Wien Museum.

Arixyleborus leprosulus Schedl 1953:300, my homotypes, lectotype in Wien Museum, compared to (=*Arixyleborus aralidii* Nunberg 1960:618) holotype in British Museum (Natural History).

Arixyleborus mediosectus (Eggers 1923: 215), originally in *Xyleboricus*, Eggers metatypes in Wien Museum compared to (=*Xyleboricus angulatus* Schedl 1942:183) lectotype in Wien Museum.

Camptocerus major (Eggers 1929:60), originally in *Loganius*, holotype in Wien Museum compared to (=*Camptocerus uniseriatus* Schedl 1972:54) holotype in Wien Museum.

Camptocerus orientalis Eggers 1943:244, male paratype in Wien Museum compared to (=*Camptocerus tectus* Eggers 1943:244) male paratype in Wien Museum.

Camptocerus suturalis (Fabricius 1801: 393), my homotypes, syntypes in Copenhagen Museum examined, compared to (=*Camptocerus hirtipennis* Schedl 1973:165) female allotype in Wien Museum.

Coccotrypes advena Blandford 1894:100, my homotypes, holotype in British Museum (Natural History) examined, compared to (=*Dendrurgus philippinensis* Eggers 1923:145) my homotypes, holotype examined, also compared to (=*Dendrurgus ternatensis* Eggers 1923:146) syntypes in Wien Museum, also compared to (=*Dendrurgus minor* Eggers 1923:150) my homotypes, lectotype examined, also compared to (=*Thamnurgides tutuilensis* Beeson 1929:229) paratypes, holotype examined.

Coccotrypes barbatus (Schedl 1934:90), originally in *Thamnurgides*, my homotypes, lectotype examined, compared to (=*Thamnurgides ater* Eggers 1936:84) one Wien Museum cotype, also compared to (=*Thamnurgides dipterocarpi* Beeson 1939:288) FRI syntypes, also compared to (=*Thamnurgides bambusae* Beeson 1939:289) FRI syntypes.

Coccotrypes carpophagus (Hornung 1842: 116), originally in *Bostrichus*, my homotypes, syntypes examined, compared to (=*Coccotrypes trevori* Beeson 1939:282) holotype in FRI, also compared to (=*Coccotrypes pilosulus* Schedl 1949:118) holotype in Wien Museum, also compared to (=*Coccotrypes ceylonicus* Schedl 1949:119) lectotype in Wien Museum, also compared to (=*Coccotrypes grisseopuberulus* Schedl 1972:59) holotype in Wien Museum, also compared to (=*Coccotrypes exasperatus* Schedl 1975:455) paratype in Wien Museum.

Coccotrypes cyperi (Beeson 1929:230), originally in *Thamnurgides*, my homotypes compared to (=*Poecilips subaplanatus* Schedl 1942:23) lectotype in Wien Museum.

Coccotrypes dactyliperda (Fabricius 1801: 387) my specimens that were compared to

Eggers homotypes compared to (=*Coccotrypes borassi* Beeson 1939:283) holotype in FRI, also compared to (=*Coccotrypes elaeocarpi* Beeson 1939:284) holotype in FRI.

Coccotrypes longior (Eggers 1927:83), originally in *Poecilips*, my homotypes, holotype examined, compared to (=*Poecilips oblongus* Eggers 1927:83) lectotype in U.S. National Museum and two paratypes in Wien Museum, also compared to (=*Poecilips nitidipennis* Schedl 1950:896) holotype in Wien Museum, also compared to (=*Poecilips apicatus* Schedl 1971:372) holotype in Wien Museum.

Coccotrypes myristicae (Roepke 1919:23), originally in *Thamnurgides*, Eggers homotypes compared to (=*Thamnurgides masoni* Beeson 1939:292) FRI syntypes.

Coccotrypes nitidus (Eggers 1923:147), originally in *Dendrurgus*, holotype in Wien Museum compared to (=*Poecilips aterrimus* Schedl 1953:298) holotype in Wien Museum.

Coccotrypes nubilus (Blandford 1894:95), originally in *Dryocoetes*, my homotypes, syntypes examined, compared to (=*Thamnurgides parvus* Beeson 1939:297) holotype in FRI, also compared to (=*Thamnurgides himalayensis* Beeson 1939:299) holotype in FRI, also compared to (=*Thamnurgides corticus* Beeson 1939:298) holotype in FRI, also compared to (=*Thamnurgides brevipilosus* Beeson 1939:298) holotype in FRI, also compared to (=*Poecilips mauritianus* Browne 1970:569) holotype in British Museum (Natural History).

Coccotrypes papuanus (Eggers 1923:148), originally in *Dendrurgus*, my homotypes, lectotype in Wien Museum examined, compared to (=*Thamnurgides rubidus* Beeson 1939:290) holotype in FRI.

Coccotrypes rhizophorae (Hopkins 1915:48), originally in *Spermatoplex*, my homotypes, lectotype in U.S. National Museum examined, compared to (=*Thamnurgides shanorum* Beeson 1939:296) holotype in FRI.

Coccotrypes salakensis (Schedl 1939:38), originally in *Poecilips*, my homotypes, lectotype in Wien Museum examined, compared to (=*Thamnurgides opacifrons* Beeson 1939:294) holotype in FRI, also compared to (=*Poecilips acuminatus* Schedl 1966:34) syntypes in Wien Museum.

Conophthorus edulis Hopkins 1915:430, holotype in U.S. National Museum compared to (=*Conophthorus cembroides* Wood 1971:74) holotype in Wood Collection.

Conophthorus resinosae Hopkins 1915:431, holotype in U.S. National Museum compared to (=*Conophthorus banksianae* McPherson 1970:1020) several paratypes in U.S. National Museum and many other specimens.

Coptoborus usagaricus (Eggers 1922:172), originally in *Xyleborus*, a paratype and Eggers homotypes compared to (=*Xyleborus usagaricus subadjunctus* Schedl 1950:28) holotype in British Museum (Natural History), also compared to (=*Streptocranus hendrickxi* Schedl 1953:245) lectotype in Wien Museum, also compared to (=*Xyleborus monticolus* Schedl 1957:113) paratypes in Wien Museum, also compared to (=*Xyleborus fallaciosus* Schedl 1957:114) paratypes in Wien Museum.

Coptodryas elegans (Sampson 1923:288), originally in *Xyleborus*, my homotypes, holotype in British Museum (Natural History) examined, compared to (=*Xyleborus concinnus* Beeson 1930:214) holotype in FRI.

Coptodryas myristicae (Schedl 1939:49), originally in *Xyleborus*, lectotype in Wien Museum compared to (=*Xyleborus theae* Eggers 1940:144) Eggers cotype in Wien Museum, also compared to (=*Xyleborus brevipilosus* Eggers 1940:145) Eggers cotype, also compared to (=*Xyleborus cylindripennis* Schedl 1954:152) lectotype in Wien Museum.

Coptodryas nugax (Schedl 1939:353), originally in *Xyleborus*, lectotype in Wien Museum compared to (=*Xyleborus fragosus* Schedl 1942:41) lectotype in Wien Museum.

Coptodryas recidens (Sampson 1923:287), originally in *Xyleborus*, my homotypes, holotype in British Museum (Natural History) examined, compared to (=*Xyleborus minutissimus* Eggers 1930:204) holotype in FRI.

Coptodryas undulatus (Sampson 1919:111), originally in *Xyleborus*, my homotypes, lectotype in British Museum (Natural History) examined, compared to (=*Xyleborus leprosulus* Schedl 1936:27) lectotype in Wien Museum.

Cryphalus major Stebbing 1903:270, holotype in FRI compared to (=*Cryphalus morinda* Stebbing 1903:265) holotype in FRI. Name selection based on first revisor's choice.

Cryphalus ruficollis Hopkins 1915:39, holotype in U.S. National Museum compared to (=*Cryphalus fraseri* Hopkins 1915:40) holotype in U.S. National Museum. This was earlier recognized by me as a subspecies of *C. ruficollis*; however, the observed variation now appears to involve gradual, primary clinal variation over vast distances and does not warrant subspecies recognition, as geographical races are now understood.

Cryphalus scabricollis Eichhoff 1878:491, holotype in Hamburg Museum examined by Beeson before it was destroyed in 1944, his homotypes were compared to (=*Cryphalus discretus* Eichhoff 1878:490) Beeson homotypes in FRI, also compared to (=*Cryphalus dilutus* Eichhoff 1878:490) Beeson homotypes in FRI. My examination of several hundred specimens in the Beeson Collection at FRI indicates that these three names all apply to the same species. The name *scabricollis* was selected for this species by first revisor's choice, because it is more descriptive of the species.

Cryphalus sylvicola (Perkins 1900:181), originally in *Hypothenemus*, my homotypes, syntypes in British Museum (Natural History) examined, compared to (=*Cryphalus swezeyi* Schedl 1942:48) lectotype in Wien Museum, also compared to (=*sylvicola obliquus* Schedl 1950:48) lectotype in Wien Museum.

Crypturgus pusillus (Gyllenhal 1813:371), my specimens compared to Eggers homotypes were compared to (=*Polygraphus minimus* Stebbing 1902:252) Stebbing and Beeson specimens of this species, syntypes apparently lost or labels removed.

Cyrtogenius lineatopunctatus (Eggers 1927: 401), originally in *Xyleborus*, this species is here transferred to *Cyrtogenius*.

Cyrtogenius luteus (Blandford 1894:94), originally in *Dryocoetes*, it is here transferred to *Cyrtogenius*, and my homotypes, syntypes in British Museum (Natural History), compared to (=*Carposinus pini* Hopkins 1915:47) holotype in U.S. National Museum.

Dryocoetes autographus (Ratzeburg 1837: 160), syntypes not located, several hundred European identified examples examined, some of them compared to (=*Dryocoetes brasiliensis* Schedl 1940:207) syntypes in Wien Museum.

Dryocoetiops laevis (Strohmeyer 1911:22), originally in *Ozopemon*, Eggers homotypes and a paratype compared to (=*Poecilips loebli* Schedl 1972:227) Schedl homotypes.

Dryocoetoides paradoxus (Schedl 1972:71), originally in *Xyleborus*, holotype in Wien Museum compared to (=*Xyleborus solitaripennis* Schedl 1976:77) holotype in Wien Museum.

Dryocoetoides pseudosolitarius (Eggers 1933:28), originally in *Xyleborus*, my homotypes, holotype in Paris Museum examined, compared to (=*Xyleborus pseudosolitarius schizolobius* Schedl 1950:179) lectotype in Wien Museum.

Eccoptopterus gracilipes (Eichhoff 1886: 25), originally in *Platydactylus*, Eggers homotypes compared to (=*Xyleborus collaris* Eggers 1923:194) my homotypes, lectotype in U.S. National Museum.

Eccoptopterus limbus Sampson 1911:381, my homotypes, holotype in British Museum (Natural History) examined, compared to (=*Xyleborus squamulatus duplicatus* Eggers 1923:193) lectotype in U.S. National Museum.

Eidophelus imitans Eichhoff 1875:201, my homotypes, one syntype in British Museum (Natural History) examined, compared to (=*Phellodendrophagus elegans* Krivolutskaya 1958:150?) specimens (paratypes?) from original series in my collection, also compared to (=*Ptilopodius nitidus* Schedl 1959:475) holotype in Wien Museum.

Ernocladius corpulentus (Sampson 1919: 113), originally in *Cryphalus*, my syntypes, holotype in British Museum (Natural History) examined, compared to (=*Margadillius corpulentus sundri* Schedl 1969:48) Schedl's "paratype," which appears to be the holotype.

Ernoporus antennarius Schedl 1974:461, my series that was compared to paratypes was compared to (=*Euptilius papuanus* Browne 1984:70) a paratype.

Euwallacea andamanensis (Blandford 1896: 222), originally in *Xyleborus*, my homotypes, holotype in British Museum (Natural History), compared to (=*Xyleborus granulipennis* Eggers 1930:194) FRI paratypes, lectotype in U.S. National Museum examined, also compared to (=*Xyleborus intextus* Beeson 1930: 211) holotype in FRI, also compared to (=*Xyleborus senachalensis* Beeson 1930:212) holotype in FRI.

Euwallacea bicolor (Blandford 1894:113), originally in *Xyleborus*, holotype in British Museum (Natural History) compared to (=*Xyleborus bicolor unimodus* Beeson 1929: 238) holotype in British Museum (Natural

History), also compared to (=*Xyleborus rodgeri* Beeson 1930:213) holotype in FRI, also compared to (=*Xyleborus rodgeri privatus* Beeson 1930:213) holotype in FRI.

Euwallacea destruens (Blandford 1896: 221), originally in *Xyleborus*, my homotypes, holotype in British Museum (Natural History), compared to (=*Xyleborus pseudobarbatus* Schedl 1942:193) syntypes in Wien Museum, also compared to (=*Xyleborus nandarivatus* Schedl 1950:52) syntypes in Wien Museum.

Euwallacea fornicatus (Eichhoff 1868:151), originally in *Xyleborus*, Eggers homotypes compared to (=*Xyleborus whitfordiodendrus* Schedl 1942:189) lectotype in Wien Museum, also compared to (=*Xyleborus perbrevis* Schedl 1951:59) holotype in Wien Museum, also compared to (=*Xyleborus schultzei* Schedl 1958:68) lectotype in Wien Museum, also compared to (=*Xyleborus tapatapaoensis* Schedl 1951:152) lectotype in Wien Museum.

Euwallacea quadraticollis (Eggers 1923: 197), originally in *Xyleborus*, my homotypes, lectotype in U.S. National Museum examined, compared to (=*Xyleborus duplicatus* Schedl 1933:102) holotype in Wien Museum.

Euwallacea sibsagaricus (Eggers 1930: 196), originally in *Xyleborus*, holotype in FRI compared to (=*Xyleborus dalbergiae* Eggers 1930:196) holotype in FRI.

Euwallacea velatus (Sampson 1913:443), originally in *Xyleborus*, my homotypes, holotype in British Museum (Natural History) examined, compared to (=*Xyleborus assamensis* Eggers 1930:195) holotype in FRI, also compared to (=*Xyleborus asperipennis* Eggers 1934:27) holotype in FRI.

Euwallacea wallacei (Blandford 1896:220), originally in *Xyleborus*, my homotypes, holotype in British Museum (Natural History) examined, compared to (=*Xyleborus siporanus* Hagedorn 1910:11) Eggers homotype, also compared to (=*Xyleborus confinis* Eggers 1923:200) lectotype in Wien Museum, also compared to (=*Xyleborus ovalicollis* Eggers 1930:193) holotype in FRI, also compared to (=*Xyleborus perakensis* Schedl 1942:194) holotype in Wien Museum.

Euwallacea xanthopus (Eichhoff 1868:151), originally in *Xyleborus*, Beeson and Eggers homotypes (holotype lost with Hamburg Museum) compared to (=*Xyleborus semirudis* Blandford 1896:210) my homotypes, holotype in British Museum (Natural History) also examined, also compared to (=*Xyleborus rudis* Eggers 1930:192) holotype in FRI, also compared to (=*Xyleborus semipilosus* Eggers 1932:300) Eggers homotypes, also compared to (=*Xyleborus neohybridus* Schedl 1942: 188) syntypes in Wien Museum, also compared to (=*Xyleborus artehybridus* Schedl 1951:66) syntypes in Wien Museum.

Gnathotrupes bituberculatus (Blandford 1904:248), originally in *Gnathotrichus*, my homotypes, lectotype in British Museum (Natural History) examined, compared to (=*Gnathotrichus impressus* Schedl 1977:44) holotype in Wien Museum.

Gnathotrupes longipennis (Blanchard 1851: 429), originally in *Tomicus*, Schedl homotypes in Wien Museum compared to (=*Gnathotrichus obnixus* Schedl 1939:47) one syntype in Wien Museum, also compared to (=*Gnathotrichus corthyloides* Schedl 1951:20) lectotype in Wien Museum, also compared to (=*Gnathotrichus corthyliformis* Schedl 1964:312) lectotype in Wien Museum, also compared to (=*Gnathotrupes constrictus* Schedl 1975:6) holotype in Wien Museum.

Gymnochilus consocius (Blandford 1897: 171), originally in *Problechilus*, my homotypes, holotype in British Museum (Natural History) examined, compared to (=*Problechilus novateutonicus* Schedl 1936:105) holotype in Wien Museum.

Hypocryphalus mangiferae (Stebbing 1914:542), originally in *Cryphalus*, my homotypes, lectotype in British Museum (Natural History) examined, compared to (=*Hypocryphalus opacus* Schedl 1942:20) lectotype in Wien Museum.

Hypocryphalus sandakanensis (Schedl 1937:548), originally in *Cryphalus*, holotype in Wien Museum compared to (=*Hypocryphalus maculatus* Browne 1961:303) holotype in British Museum (Natural History).

Hypothenemus areccae (Hornung 1842: 117), originally in *Bostrichus*, my homotypes, lectotype in Berlin Museum examined, compared to (=*Stephanoderes bambesanus* Eggers 1940:232) cotype in Wien Museum, also compared to (=*Hypothenemus bauhaniae* Schedl 1950:19) lectotype in Wien Museum, also compared to (=*Stephanoderes occidentalis* Schedl 1954:76) lectotype in Wien Museum.

Hypothenemus birmanus (Eichhoff 1878: 486) originally in *Triarmocerus*, my homotypes, holotype in Wien Museum examined, compared to (=*Stephanoderes nibarani* Beeson 1933:10) holotype in FRI, also compared to (=*Stephanoderes ampliatus* Eggers 1936:627) one cotype in Wien Museum, holotype in British Museum (Natural History) examined.

Hypothenemus californicus Hopkins 1915: 19, my homotypes, holotype in U.S. National Museum examined, compared to (=*Stephanoderes zeae* Schedl 1973:169) paratypes in Wien Museum. This is an obvious introduction into America from Africa, Asia Minor, or southern Europe; however, it has not yet been associated with a synonym from those areas.

Hypothenemus crudiae (Panzer 1791:35), originally in *Bostrichus*, my series and Eggers homotypes compared to (=*Cryphalus mucronifer* Wollaston 1867:116) syntypes in British Museum (Natural History).

Hypothenemus donisi (Schedl 1957:46), originally in *Ericryphalus*, paratypes in Wien Museum compared to (=*Ericryphalus madagascariensis* Schedl 1961:131) paratypes in Wien Museum.

Hypothenemus eruditus Westwood 1836: 34, my homotypes, syntypes in British Museum (Natural History) examined, compared to (=*Cryphalus tectonae* Stebbing 1903:263) syntypes in FRI, also compared to (=*Cryphalus striatopunctatus* Lea 1910:142) Schedl homotypes in Wien Museum, also compared to (=*Cryphalus tantillus* Lea 1910:142) Schedl homotypes in Wien Museum, also compared to (=*Hypothenemus tuberculosus* Hagedorn 1912:339) one paratype in Wien Museum, also compared to (=*Hypothenemus pusillus* Eggers 1927:173) holotype in U.S. National Museum, also compared to (=*Hypothenemus argentinensis* Schedl 1939:408) lectotype in Wien Museum, also compared to (=*Hypothenemus cylindricus* Schedl 1939: 409) lectotype in Wien Museum, also compared to (=*Hypothenemus asaroriensis* Beeson 1940:195) holotype in FRI, also compared to (=*Hypothenemus maniensis* Schedl 1941:110) lectotype in Wien Museum, also compared to (=*Stephanoderes nanulus* Schedl 1949:263) lectotype in Wien Museum, also compared to (=*Hypothenemus parilis* Schedl 1951:100) lectotype in Wien Museum, also compared to (=*Hypothenemus obscuriceps* Schedl 1951:449) lectotype in Wien Museum, also compared to (=*Stephanoderes tigrensis* Schedl 1952:452) lectotype in Wien Museum, also compared to (=*Hypothenemus parcius* Schedl 1957:49) paratypes in Wien Museum, also compared to (=*Hypothenemus cylindripennis* Schedl 1957:51) one paratype in Wien Museum, also compared to (=*Hypothenemus vianai* Schedl 1958:42) lectotype in Wien Museum, also compared to (=*Hypothenemus mesoleius* Schedl 1959:480) syntypes in Wien Museum, also compared to (=*Hypothenemus minutulus* Schedl 1972: 225) paratypes in Wien Museum, also compared to (=*Cryphalus minutus* Schedl 1978:299) holotype in Wien Museum.

Hypothenemus fuscicollis (Eichhoff 1878: 148), originally in *Stephanoderes*, Eggers homotype in Wien Museum compared to (=*Stephanoderes sundaensis* Eggers 1927: 396) holotype in Wien Museum, also compared to (=*Hypothenemus ghanaensis* Schedl 1962:67) one paratype in Wien Museum.

Hypothenemus hampei (Ferrari 1867:11, 12), originally in *Cryphalus*, syntypes in Wien Museum examined, compared to (=*Stephanoderes glabellus* Schedl 1951:452) lectotype in Wien Museum.

Hypothenemus ingens (Schedl 1942:18), originally in *Stephanoderes*, lectotype in Wien Museum compared to (=*Cryphalomorphus grandis* Schedl 1971:10) holotype in Wien Museum.

Hypothenemus plumeriae (Nördlinger 1856:74), originally in *Bostrichus*, holotype in Wien Museum compared to (=*Stephanoderes cylindricus* Hopkins 1915:25) my homotypes, holotype in U.S. National Museum examined, also compared to (=*Hypothenemus guadeloupensis* Schedl 1951:98) syntypes in Wien Museum, also compared to (=*Stephanoderes ituriensis* Schedl 1957:55) syntypes in Wien Museum.

Hypothenemus pubescens Hopkins 1915: 19, my homotypes, holotype in U.S. National Museum, compared to (=*Hypothenemus minutissimus* Schedl 1951:450) lectotype in Wien Museum.

Hypothenemus seriatus (Eichhoff 1872: 133), originally in *Stephanoderes*, my homotypes, lectotype in Brussels Museum, compared to (=*Cryphalus aulmanni* Hagedorn 1912:41) Eggers homotypes in Wien Museum, also compared to (=*Hypothenemus cassavaensis* Schedl 1938:453) lectotype in Wien Museum, also compared to (=*Stephanoderes hawaiiensis* Schedl 1941:112) syntypes in Bishop and Wien museums, also compared to (=*Hypothenemus striatulus* Schedl 1942: 12) lectotype in Wien Museum, also compared to (=*Hypothenemus marovoayi* Schedl 1953:81) lectotype in Wien Museum, also compared to (=*Stephanoderes asperatus* Schedl 1967:226) paratypes in Wien Museum.

Hypothenemus stigmosus (Schedl 1951: 101), originally in *Stephanoderes*, holotype in Wien Museum compared to (=*Stephanoderes garciae* Schedl 1958:42) holotype in Wien Museum.

Leptoxyleborus concisus (Blandford 1894: 107), originally in *Xyleborus*, my homotypes, holotype in British Museum (Natural History), compared to (=*Xyleborus incurvus* Eggers 1930:197) holotype in FRI.

Leptoxyleborus depressus (Eggers 1923: 190), originally in *Xyleborus*, holotype in Wien Museum compared to (=*Xyleborus sejugatus* Schedl 1942:188) Schedl homotype in Wien Museum.

Leptoxyleborus semigranulatus (Schedl 1931:340), originally in *Xyleborus*, holotype in Wien Museum compared to (=*Xyleborus artemarginatus* Schedl 1975:456) holotype in Wien Museum.

Monarthrum chapuisi Kirsch 1866:213, holotype in Berlin Museum compared to (=*Monarthrum bolivianum* Eggers 1935:80) my homotype, holotype in U.S. National Museum examined.

Monarthrum ingens (Eichhoff 1869:278), originally in *Pterocyclon*, my homotypes, holotype in Brussels Museum examined, compared to (=*Pterocyclon assequens* Schedl 1978:302) holotype in Wien Museum.

Pityophthorus deodara (Stebbing 1903: 274), originally in *Cryphalus*, syntypes in FRI compared to (=*Cryphalus himalayensis* Stebbing 1914:540) syntypes in FRI, also compared to (=*Pityophthorus sampsoni* Stebbing 1914:551) syntypes in FRI.

Sauroptilius sauropterus (Schedl 1953: 101), male holotype in Wien Museum and others in British Museum (Natural History) examined, holotype compared to (=*Xyleborus sauropteroides* Schedl 1970:237) female paratype in Wien Museum. These obviously are opposite sexes of the same species.

Scolytogenes knabi (Hopkins 1915:34), my homotypes, holotype in U.S. National Museum, compared to (=*Cryphalomorphus alienus* Schedl 1976:65) holotype in Wien Museum. This species was collected by me in Japan in 1980, but I have not yet associated it with a name from that area. It obviously has been carried through commerce to many areas, but it has not yet been cited under this name outside America.

Scolytomimus pusillus (Eggers 1927:88), originally in *Neoxyloctonus*, my homotypes, lectotype in U.S. National Museum examined, compared to (=*Scolytomimus kalshoveni* Schedl 1940:132) one paratype in Wien Museum and my topotypes from the original series, also compared to (=*Scolytocleptes insularis* Schedl 1962:491) holotype in Wien Museum.

Scolytoplatypus mikado Blandford 1893: 437, my homotypes, syntypes in British Museum (Natural History) examined, compared to (=*Scolytoplatypus sinensis* Tsai & Huang 1965:123) my paratypes.

Scolytoplatypus papuanus Eggers 1923: 165, my homotypes, male homotype and female allotype in Wien Museum examined, compared to (=*Scolytoplatypus luzonicus* Eggers 1935:244) holotype in U.S. National Museum.

Scolytoplatypus siomio Blandford 1893: 436, my homotypes, syntypes in British Museum (Natural History) examined, compared to (=*Scolytoplatypus kunala* Strohmeyer 1908:161) holotype in Strohmeyer Collection.

Scolytopsis puncticollis Blandford 1896: 123, my homotypes, syntypes in British Museum (Natural History) examined, compared to (=*Scolytopsis cubensis* Wood 1961:87) holotype in U.S. National Museum. The type series of *S. cubensis* apparently developed under adverse environmental conditions that resulted in abnormally small specimens. Series from Cuba examined subsequently bridge both the size and character gaps.

Terminalinus crucipennis (Schedl 1962: 277), originally in *Xyleborus*, holotype in Wien Museum compared to (=*Xyleborus metacrucifer* Browne 1965:201) my homotype, holotype in British Museum (Natural History) examined.

Terminalinus hirtus (Hagedorn 1904:126), originally in *Xyleborus*, Beeson homotypes and other series in FRI compared to (=*Xyleborus hirtuosus* Beeson 1930:217) syntypes in FRI.

Trypodendron laeve Eggers 1939:122, syntypes in Wien Museum compared to (=*Trypodendron piceum* Strand 1946:172) Eggers homotypes (or paratypes?) in Wien Museum.

Theoborus ricini (Eggers 1932:298), originally in *Xyleborus*, my homotypes, holotype in U.S. National Museum examined, compared to (=*Xyleborus solitariceps* Schedl 1954:45) lectotype in Wien Museum.

Webbia quattuordecimspinatus (or *14-spinatus*) Sampson 1921:34, my homotypes and male holotype in British Museum (Natural History) compared to (=*Webbia quattuordecimspinatus* or *14-spinatus* Schedl 1942:182) female syntypes in British Museum (Natural History) and Wien Museum. Schedl appears to have inadvertently validated a new name and homonym when his intent was to describe the opposite sex of Sampson's species.

Xyleborinus andrewesi (Blandford 1896: 227), originally in *Xyleborus*, my homotypes, holotype in British Museum (Natural History) examined, compared to (=*Xyleborus persphenos* Schedl 1970:219) one paratype in Wien Museum.

Xyleborinus artestriatus (Eichhoff 1878: 507), originally in *Xyleborus*, my series, Eggers homotypes compared to (=*Xyleborus rugipennis* Schedl 1953:303) lectotype in Wien Museum.

Xyleborinus gracilis (Eichhoff 1868:145), originally in *Xyleborus*, my series, Eggers homotypes (holotype lost) compared to (=*Xyleborus neogracilis* Schedl 1954:46) lectotype in Wien Museum.

Xyleborinus saxeseni (Ratzeburg 1837:167), originally in *Bostrichus*, Eggers and Schedl homotypes (syntypes not located) compared to (=*Xyleborus subspinosus* Eggers 1930:203) holotype in FRI, also compared to (=*Xyleborus pseudogracilis* Schedl 1937:169) lectotype in Wien Museum, also compared to (=*Xyleborus retrusus* Schedl 1940:208) lectotype in Wien Museum, also compared to (=*Xyleborus paraguayensis* Schedl 1949:276) holotype in Wien Museum, also compared to (=*Xyleborus cinctipennis* Schedl 1980:186) holotype in Wien Museum.

Xyleborus adelographus Eichhoff 1868: 400, my series and Eggers homotypes (syntypes lost) compared to (=*Xyleborus accomodatus* Schedl 1966:112) holotype in Wien Museum.

Xyleborus adusticollis (Motschulsky 1863: 514), originally in *Tomicus*, holotype in Moscow Institute of Zoology examined and sketched (=*Xyleborus vestitus* Schedl 1931: 341), holotype in Wien Museum compared to my specimen. The uniqueness of this species, my notes and diagrams, and the locality leave little doubt as to the identity of this species.

Xyleborus approximatus Schedl 1951:77, syntypes in Wien Museum compared to (=*Xyleborus potens* Schedl 1964:298) Schedl homotype in Wien Museum.

Xyleborus biconicus Eggers 1928:97, my homotypes, holotype in U.S. National Museum examined, compared to (=*Xyleborus bicinctus* Schedl 1972:69) holotype in Wien Museum, also compared to (=*Xyleborus bicinctulus* Schedl 1974:338) holotype in Wien Museum.

Xyleborus bidentatus (Motschulsky 1863: 514), originally in *Phloeotrogus*, my homotypes, holotype in Moscow Institute of Zoology, compared to (=*Xyleborus quadridens* Eggers 1930:191) holotype (an aberration) in FRI.

Xyleborus caraibicus Eggers 1941:103, my homotypes, holotype in U.S. National Museum, compared to (=*Xyleborus variabilis* Schedl 1949:281) syntypes in Wien Museum.

Xyleborus crinitus Schedl 1962:301, my homotype, holotype in Wien Museum examined, compared to (=*Xyleborus nigericus* Browne 1970:572) holotype in British Museum (Natural History).

Xyleborus emarginatus Eichhoff 1878:510, my series, Eggers homotypes examined (holotype lost), compared to (=*Xyleborus emarginatus semicircularis* Schedl 1973:92) paratypes in Wien Museum.

Xyleborus eximius Schedl 1970:362, my specimens, paratypes in Wien Museum examined, compared to (=*Xyleborus apicenotatus* Schedl 1971:377) holotype in British Museum (Natural History).

Xyleborus fallax Eichhoff 1878:508, my homotypes, holotype in Brussels Museum, compared to (=*Xyleborus amphicranulus* Eggers 1923:204) syntypes in Wien Museum.

Xyleborus ferrugineus (Fabricius 1801: 388), originally in *Bostrichus*, my homotypes, lectotype in Copenhagen Museum, compared to (=*Xyleborus rufopiceus* Eggers 1932:303) one paratype in Wien Museum.

Xyleborus grossmanni Schedl 1952:362, holotype in Wien Museum compared to (=*Xyleborus acuminatus* Schedl 1970:94) holotype in Wien Museum.

Xyleborus mascareniformis Eggers 1927: 400, my specimens, Eggers homotype examined, compared to (=*Xyleborus onerosus* Schedl 1942:185) holotype in British Museum (Natural History).

Xyleborus multispinatus Eggers 1920:125, lectotype in Wien Museum compared to (=*Xyleborus acanthus* Schedl 1951:15) paratypes in Wien Museum.

Xyleborus mutabilis Schedl 1935:92, holotype in Wien Museum compared to (=*Xyleborus itatiayaensis* Schedl 1936:109) lectotype in Wien Museum.

Xyleborus perforans (Wollaston 1857:96), originally in *Tomicus*, my homotypes, syntypes in British Museum (Natural History) examined, compared to (=*Xyleborus criticus* Schedl 1950:899) lectotype in Wien Museum.

Xyleborus perlongus Eggers 1943:386, holotype in Wien Museum compared to (=*Xyleborus pulcnerrimus* Schedl 1949:38) holotype in Wien Museum, also compared to (=*Xyleborus pulcheripes* Schedl 1958:46) holotype in Wien Museum.

Xyleborus similis Ferrari 1867:23, my homotypes, holotype in Wien Museum examined and compared to (=*Xyleborus novaguineanus* Schedl 1936:530) holotype in Wien Museum, also compared to (=*Xyleborus dilatatulus* Schedl 1953:127) lectotype in Wien Museum.

Xyleborus subcostatus Eichhoff 1869:281, my specimens, holotype in Brussels Museum examined, compared to (=*Xyleborus subcostatus dearmatus* Eggers 1923:205) holotype in Wien Museum. This synonym represents no more than an aberration.

Xyleborus sulcicauda Schedl 1972:271, holotype in Wien Museum compared to (=*Xyleborus tenuipennis* Browne 1974:71) Schedl homotype, holotype in British Museum (Natural History).

Xyleborus volvulus (Fabricius 1775:454), originally in *Bostrichus*, my homotypes, lectotype in Copenhagen Museum examined, compared to (=*Xyleborus silvestris* Beeson 1929:241) holotype in British Museum (Natural History), also compared to (=*Xyleborus granularis* Schedl 1950:898) lectotype in Wien Museum.

Xylosandrus ater (Eggers 1923:210), originally in *Xyleborus*, Eggers homotype compared to (=*Xyleborus retusiformis* Schedl 1936:31) holotype in Wien Museum.

Xylosandrus cylindrotomicus (Schedl 1939: 40), originally in *Pseudoxyleborus*, lectotype in Wien Museum compared to (=*Xyleborus semitruncatus* Schedl 1942:115) lectotype in Wien Museum, also compared to (=*Xyleborus ramulorum* Schedl 1957:115) paratype in Wien Museum.

Xylosandrus mutilatus (Blandford 1894: 103), originally in *Xyleborus*, my syntypes, holotype in British Museum (Natural History), compared to (=*Xyleborus sampsoni* Eggers 1930:184) holotype in FRI.

NEW NAMES

Treated below are names of Scolytidae that are regarded as junior homonyms of available names. The new names are presented in alphabetical order for ease of reference. Each name is followed by a citation of the original combination, author, year and page of validation, kind and sex of type, type locality, and type repository. This is followed by a brief statement of the action taken and a proposal for a new name. A complete reference to these citations (author, date, page) is presented at the end of this article in order to meet requirements of the code. These and other references used here may also be found in Wood and Bright (1987).

Araptus frontis, n. n.

Gnathocranus frontalis Schedl 1978:302 (Holotype, female; Brasilien, Encruzilhada, Bahia; Wien Museum). *Preoccupied*

The transfer of *Gnathocranus frontalis* Schedl 1978:302 to *Araptus* by Wood (1986:97) made it a junior homonym of *A. frontalis* Wood 1974:52 that must be replaced. The new name *frontis* is proposed as a replacement for the 1978 name as indicated above.

Araptus guadeloupanus, n. n.

Brachydendrulus guadeloupensis Schedl 1970:91 (Holotype, sex?; Guadeloupe; Wien Museum). *Preoccupied*

The transfer of *Brachydendrulus guadeloupensis* Schedl 1970:91 to *Araptus* by Wood (1986:97) made this name a junior homonym of *A. guadeloupensis* Schedl 1951:73, a junior synonym of *A. laevigatus* (Eggers). Even though it is a synonym, the 1951 name is available and requires that the 1970 name be replaced. The new name *guadeloupanus* is proposed as a replacement as indicated above.

Coccotrypes brunnipes, n. n.

Coccotrypes brunneus Nunberg 1973:23 (Holotype, female; Congo Belge: P.N.A., Mont Hoyo, Grotte Yolohafiri, 1,030 m). *Preoccupied*

The name *Coccotrypes brunneus* Nunberg 1973:23 is preoccupied by *C. brunneus* (Nunberg 1960:616), formerly in *Poecilips*, and must be replaced. The new name *brunnipes* is proposed as a replacement as indicated above.

Coccotrypes robustulus, n. n.

Poecilips robustus Schedl 1972:227 (Holotype, female; Ceylon, Matale, 400 m; Museum d'Histoire Naturelle de Geneve). *Preoccupied*

The name *Coccotrypes robustus* (Schedl 1972:227), formerly in *Poecilips*, is preoccupied by *C. robustus* Eichhoff 1878:313 and must be replaced. The new name *robustulus* is proposed as a replacement as indicated above.

Coccotrypes striatulus, n. n.

Thamnurgides striatus Eggers 1927:82 (Holotype, female; Philippinen: Luzon, Provinz Laguna, Mount Maquiling; U.S. National Museum). *Preoccupied*

The name *Coccotrypes striatus* (Eggers 1927:82), formerly in *Thamnurgides*, is preoccupied by *C. striatus* Eggers 1920:33 and must be replaced. The new name *striatulus* is proposed as a replacement as indicated above.

Hypothenemus aterrimulus, n. n.

Lepiceroides aterrimus Schedl 1957:59 (Holotype, female; Ruanda: Ihembe; Tervuren Museum). *Preoccupied*

The Schedl paratypes of *Lepiceroides aterrimus* Schedl 1957:59 were examined and found (Wood 1986:92) to represent the genus *Hypothenemus*. The transfer made this species a junior homonym of *H. aterrimus* Schedl 1951:104 and must be replaced. The new name *aterrimulus* is proposed as a replacement for the 1957 name as indicated above.

Hypothenemus ruginosus, n. n.

Pachynoderes rugifer Schedl 1977:395 (Holotype, female: Südafrika: Potgietersrust, Transvaal; Wien Museum). *Preoccupied*

The transfer of *Pachynoderes rugifer* Schedl 1977:395 to *Hypothenemus* (Wood 1986:92) made it a junior homonym of *H. rugifer* (Schedl 1965:9) and must be replaced. The new name *ruginosus* is proposed for the 1977 name as indicated above.

Mimiocurus monticulus, n. n.

Mimiocurus montanus Schedl 1957:73 (Holotype, sex?; Congo Belge: Kivu, Hembe-Bitale; Tervuren Museum). *Preoccupied*

The name *Mimiocurus montanus* Schedl 1957:73 became a junior homonym when *M. montanus* (Schedl 1957:71), page priority, was transferred (Wood 1986:97) to this genus from *Micracidendron*, and must be replaced. The new name *monticulus* is proposed as a replacement as indicated above.

Monarthrum boliviensis, n. n.

Cosmocorynus bolivianus Schedl 1970:103 (Holotype, female; Bolivia, Yungas del Palmar, 2,000 m; Wien Museum). *Preoccupied*

The transfer of *Cosmocorynus bolivianus* Schedl 1970:103 to *Monarthrum* (Wood 1986:99) made it a junior homonym of *Monarthrum bolivianum* Eggers 1935:80, an available name that is currently treated as a synonym of *M. chapuisi* Kirsch. The new name *boliviensis* is proposed as a replacement for the 1970 name as indicated above.

Monarthrum dentatulum, n. n.

Monarthrum dentatum Eggers 1935:84 (Holotype, male; Bolivien, Cochabamba; U.S. National Museum). *Preoccupied*

Monarthrum dentatum Eggers 1935:84 became a junior homonym when *Amphicranus dentatum* Eggers 1931:19 was transferred to *Monarthrum* by Wood (1982:1216). The new name *dentatulum* is proposed as a replacement for the 1935 name as indicated above.

Monarthrum sexdenticulum, n. n

Anchonocerus sexdentatus Eggers 1935:331 (Holotype, male; Columbien, Aguatal; U.S. National Museum). *Preoccupied*

When the name *Anchonocerus sexdentatus* Eggers 1935:331 was transferred by Wood (1986:99) to *Monarthrum*, it became a junior homonym of *Monarthrum sexdentatum* Eggers 1935:83 and must be replaced. The new name *sexdenticulum* is proposed as a replacement as indicated above.

Pityophthorus abietinus, n. n.

Pityophthorus abietis Kurenzov 1941:179, 234 (Lectotype, sex?; S Coast (Primorsky) region, Voroshilovsk district; Mountainous Taiga Station, Institute of Zoology, Academy of Science, Vladivostok, designated by Michalski 1969:895). *Preoccupied*
Pityophthorus sibiricus Nunberg 1956:208 (Automatic, replacement name for *P. abietis* Kurenzov). *Preoccupied*

The name *Pityophthorus abietis* Kurenzov 1941:179, 234 is preoccupied by *P. abietis* Blackman 1928:49 (a synonym of *P. opaculus* LeConte), and *P. sibericus* Nunberg 1956:208 is preoccupied by *P. micrographus sibiricus* Stark 1952:344 (also recognized as a subspecies by Pfeffer 1976:335). Because both names are preoccupied, the new name *abietinus* is proposed as a replacement as indicated above.

Pityophthorus brighti, n. n.

Pityophthorus blackmani Bright 1977:521 (Holotype, female; Amecameca, Mexico, Mexico; U.S. National Museum). *Preoccupied*

The name *Pityophthorus blackmani* Bright 1977:521 became a junior homonym when *Conophthocranulus blackmani* Schedl 1935:344 was transferred (Wood 1986:98) to *Pityophthorus*. Dr. Bright was notified of the homonymy and asked that I propose a new name here. The new name *brighti* is proposed as a replacement for the 1977 name as indicated above.

Pityophthorus micrographinus, n. n.

Breviophthorus micrographus Schedl 1972:60 (Holotype, sex?; Brasilien, Jacareacanga, Para; Wien Museum). *Preoccupied*

When *Breviophthorus micrographus* Schedl 1972:60 was transferred (Wood 1986:98) to *Pityophthorus*, this species became a junior homonym of *P. micrographus* (Linnaeus 1758:355) and must be replaced. The new name *micrographinus* is proposed as a replacement as indicated above.

Pityophthorus subsimilans, n. n.

Breviophthorus subsimilis Schedl 1966:104 (Holotype, sex?; Brasilien, Rio Caraguata, Matto Grosso; Wien Museum). *Preoccupied*

The transfer of *Breviophthorus subsimilis* Schedl 1966:104 to *Pityophthorus* (Wood 1986:98) made this name a junior homonym of *P. subsimilis* Schedl 1955:25 and must be replaced. The new name *subsimilans* is proposed as a replacement as indicated above.

Scolytogenes papuensis, n. n.

Xylocryptus papuanus Schedl 1975:352 (Holotype, sex?; Upper Manki L.A., Bulolo, Morobe District, New Guinea; Wien Museum). *Preoccupied*

When *Xylocryptus papuanus* Schedl 1975:352 was transferred to *Scolytogenes* (Wood 1986:90), it became a junior homonym of *S. papuanus* (Schedl 1974:459), formerly in *Cryphalophilus*, and must be replaced. The new name *papuensis* is proposed as a replacement as indicated above.

NEW TAXA

Cryphalus dipterocarpi, n. sp.

This species was designated as *Hypocryphalus dipterocarpi* Beeson 1941:288, a nomen nudum, and has been cited under that name, although it has never been validated. It is distinguished from other Indian species by the transverse carina on the male vertex, by the pointed, almost hairlike ground setae on the basal half of the elytral disc, by the moderately slender body, by the distinctive, long, elytral vestiture, and by other characters described below. It is somewhat allied to *Cryphalus strohmeyeri* Stebbing, although it is not closely related.

MALE.— Length 1.6 mm (paratypes 1.6–1.8 mm), 2.4 times as long as wide; color pale yellowish brown.

Frons broadly convex, sometimes with a weak median granule on epistoma; surface finely punctured and almost smooth and shining below upper level of eyes, almost impunctate above eyes, a subacute, conspicuous, transverse carina on vertex occupying more than median two-thirds. Vestiture fine, hairlike, restricted to area below carina, short except moderately long on epistoma. Antennal club rather small, sutures straight to very weakly procurved.

Pronotum 1.04 times as long as wide; sides subparallel and feebly arcuate on basal half, anterior margin moderately rounded and armed by six rather coarse serrations; summit slightly behind middle, asperities rather coarse, moderately abundant; posterior areas smooth, shining, finely, closely punctured. Ground vestiture not evident, erect hair sparse, moderately long on or near margins.

Elytra 1.3 times as long as wide; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae evident on basal half of disc, obsolete behind, punctures distinctly impressed at base, fading in size and depth behind; interstriae at base three to four times as wide as striae, surface smooth, shining. Declivity rather steep, convex; sculpture as on posterior disc. Vestiture of abundant ground cover of short, rather slender hair, becoming basally stouter toward declivity, shorter and as pointed scales on declivity; interstrial rows of fine, erect, hairlike setae, each seta on disc slightly longer than distance between rows or spacing within a row, on declivity some setae almost twice as long.

Female.— Similar to male except carina absent from vertex, frons more uniformly convex and more coarsely punctured; erect setae on elytra apparently slightly shorter.

Type material.— The male holotype, female allotype, and nine paratypes were taken at Margherita Factory, Lakhimpur, Assam, from *Dipterocarpus pilosus*, by B. M. Bhatia. The holotype and allotype were taken on 14 January 1936, the paratypes on 13 January 1936. The holotype and allotype are in the Forest Research Institute, Dehra Dun; the paratypes are in my collection. There are many other specimens at FRI bearing the same or similar data, as well as a series labeled Inthabaing, Insein, Burma 31-XII-1926, from the same host, none of which could be included in the type series.

Cryphalus felis, n. sp.

This species is allied to *dipterocarpi* Wood, although the relationship is not close. It is distinguished from that species by the larger size, by the stouter body form, by the longer, much more abundant ground and erect hair, and by other characters described below. This is *Cryphalus felus* Beeson, nomen nudum, that has been cited in the literature.

Male.— Length 2.0 mm (paratypes 1.9–2.0 mm), 2.1 times as long as wide; color a rather light brown.

Frons very broadly convex, surface finely rugose-reticulate to well above eyes; punctures fine, obscure; vertex with a weak, shining, poorly developed, transverse carina on median third, reticulate above carina. Vestiture inconspicuous, of sparse, fine, short and long hairlike setae.

Pronotum 0.83 times as long as wide; widest on basal fourth, outline obscurely triangular; anterior margin somewhat narrowly rounded and armed by six to eight small asperities; summit on basal fourth, asperities rather numerous, moderately large; posterior and lateral areas somewhat rugose, obscurely reticulate, punctures fine, rather obscure. Vestiture of fine, rather long hair.

Elytra 1.4 times as long as wide; outline about as in *dipterocarpi*; striae weakly indicated on basal third, minute punctures obscurely indicated almost to declivity; interstriae many times wider than striae, surface smooth, shining, punctures very small, confused. Declivity moderately steep, convex. Vestiture of fine, abundant, long hair, ground setae more abundant and half as long as erect setae; long setae in obscure rows toward declivity, some of them three or more times as long as distance between rows.

Female.— Similar to male except carina not evident on vertex, pronotal asperities slightly larger.

Type material.— The male holotype, female allotype, and three paratypes are from Mussoorie, U.P., India, R.R.D. 737, B.C.R. 108, cage 600, from *Vitis* sp., C.F.C. Beeson; one paratype emerged 1-IX-1927, the holotype and one paratype on 2-IX-1927, and the allotype and one paratype on 6-IX-1927. The holotype and allotype are in the Forest Research Institute, Dehra Dun, the paratypes in my collection. There are many other specimens in FRI under this name that could not be included in the type series.

Cryphalus fulmineus, n. sp.

This is *Cryphalus fulmineus* Beeson, nomen nudum, that has been cited in the literature. In the Indian fauna it is most nearly allied to *dorsalis* (Motschulsky) (=*indicus* Eichhoff), but it is distinguished by the more slender body form, by the absence of a transverse carina on the male vertex, by the very different epistomal area, by the host, and by other characters described below.

Male.— Length 1.8 mm (paratypes 1.8–2.2 mm), 2.1 times as long as wide; color light brown.

Frons very broadly convex, a slight, almost flat impression in median area just above epistoma; vertex without a transverse carina;

surface rather strongly reticulate, some reticulation near epistoma in median area usually organized into feeble aciculation; punctures moderately coarse, indistinct. Antennal club rather broad, segment 1 very short, sutures distinctly procurved.

Pronotum 0.86 times as long as wide; general outline and asperities much as in *dipterocarpi*; anterior margin armed by six serrations, median pair usually much longer; posterior areas finely, closely granular, a few fine, obscure punctures in lateral areas. Vestiture hairlike, erect, not abundant, longer near lateral and anterior margins.

Elytra 1.4 times as long as wide; sides almost straight and parallel on more than basal two-thirds, rather broadly rounded behind; striae not impressed, punctures very fine, shallow, distinct, not close; interstriae almost smooth and shining, with numerous, very fine, confused punctures. Declivity steep, convex. Vestiture consisting of a ground cover of abundant, short scales, each scale slightly longer than wide and apically truncate; rows of erect setae extend almost to base, each moderately slender and spaced within and between rows by distances greater (1:1.25) than length of a seta.

Female.— Similar to male except averaging slightly larger, pronotal asperities slightly larger.

Type material.— The male holotype and female allotype (both mounted on one pin) and 11 paratypes were taken at Tharali, Garhwal, U.P., India, R.R.D. 185, B.C.R. 20, cage 760, from *Alnus nitida*. The holotype and allotype emerged 25-VI-1937, the paratypes 26-28-29-VI-1937. Two paratypes are labeled Jubal, Simla, Punjab, 17-V-1924, 6000′, C.F.C. Beeson. The holotype and allotype are in the Forest Research Institute, Dehra Dun; the paratypes are in my collection. Many more specimens of this species are in FRI.

Gnathotrupes colaphus, n. sp.

This species is distinguished from *crecentus* Wood by the larger, more slender body form, by the more convex and more finely armed elytral declivity, and by the much longer declivital vestiture.

Male.— Length 2.2 mm (paratypes 2.0–2.3 mm), 3.4 times as long as wide; color light brown, areas on elytra darker.

Frons as in *crecentus* except sparse punctures much larger, slightly more numerous.

Pronotum 1.3 times as long as wide, otherwise as in *crecentus*.

Elytra 2.3 times as long as wide; outline and disc about as in *crecentus*. Declivity confined to less than posterior fourth, not as steep as *crecentus*, broadly convex; strial punctures very small, obscure; interstriae each with several minute granules from base to apex, none of them dominant. Vestiture confined to declivity, consisting of fine, confused hair of variable length, longest setae at least equal to combined width of three interstriae.

Female.— Similar to male except serrations on anterior margin of pronotum not as high or as numerous.

Type material.— The male holotype, female allotype, and 25 paratypes were taken on 9-XII-1969 at La Carbonera Experimental Forest, 50 km W Merida, Merida, Venezuela, 2500 m, No. 176, from an unidentified log, by me; 3 paratypes bear data as on the type except 27-X-1969, No. 91; 8 paratypes bear data as on the type except 28-IV-1970, No. 449, *Nectandra* sp.; 2 paratypes are from La Mucuy, Merida, Venezuela, 20-X-1969, 2500 m, No. 74, unidentified log, by me. The holotype, allotype, and paratypes are in my collection.

Gnathotrupes nectandrae, n. sp.

All series of this species were taken from the same logs that contained *colaphus* Wood, to which it is allied. This species is distinguished by the larger size, by the distinctive frons, and by the very different elytral declivity that is described below.

Male.— Length 3.0 mm (paratypes 2.8–3.1 mm), 3.3 times as long as wide; color dark brown.

Frons convex, distinctly inflated on central area from small tubercle on epistomal margin to well above eyes, a few punctures on lateral thirds, central area smooth, shining, impunctate; vestiture restricted to sparse setae on epistomal margin. Antennal sutures strongly procurved.

Pronotum 1.2 times as long as wide, as in *colaphus*.

Elytra 2.1 times as long as wide; outline and disc about as in *elaphus*. Declivity very steep, flattened, almost as in *crecentus* Wood; a small tubercle at base of interstriae 2, much smaller granules at bases of 3 and 4, two or three minute granules scattered near center of lateral face. Vestiture about as in *crecentus*.

FEMALE.— Similar to male in all respects except segmentation of abdomen.

TYPE MATERIAL.— The male holotype, female allotype, and 14 paratypes were taken at La Carbonera Experimental Forest, 50 km W Merida, Merida, Venezuela, 9-XII-1969, 2500 m, No. 176, from an unidentified log, by me; 10 paratypes bear data as on the type except 23 or 28-IV-1970, No. 449, *Nectandra* sp.; 2 paratypes are from La Mucuy, Merida, Venezuela, 20-X-1969, 2500 m, No. 74, from an unidentified log, by me. The holotype, allotype, and paratypes are in my collection.

Mimiocurus beesoni, n. sp.

This is the second member of this genus named outside of Africa. It is distinguished from other known species by the small size, by the unique male frons as described below, and by the almost scalelike elytral setae.

MALE.— Length 1.4 mm (paratypes 1.2–1.4 mm), 3.0 times as long as wide; color yellowish brown.

Frons narrow above, half as wide as width of eye, shallowly concave, surface minutely rugose, impunctate, glabrous; a strongly elevated, subacute, transverse carina at upper level of eyes. Antennal club large, oval, distinctly longer than wide, devoid of sutures, minutely pubescent to base. Eyes very large, coarsely faceted.

Pronotum 0.94 times as long as wide; widest on basal third, sides arcuately converging to narrowly rounded anterior margin; anterior margin armed by two subcontiguous, slender serrations; summit at middle; asperities coarse, moderately abundant; posterior areas smooth, shining, punctures very minute, sparse. Vestiture of very sparse, fine, short hair.

Elytra 2.0 times as long as wide, 2.0 times as long as pronotum; sides almost straight and parallel on basal three-fourths, rather broadly rounded behind; striae not evident on disc, punctures minute, moderately abundant, strongly confused. Declivity moderately steep, shallowly sulcate; sculpture as on disc; sulcus about one-third elytral width, moderately shallow, lateral margins rounded, unarmed. Vestiture of ground cover of very short, rather stout hair, and erect scales; scales in three interstrial rows on declivity, rows 1 and 2 extend forward to middle of disc, a few supplemental scales in lateral areas near apex, each scale about four times as long as wide.

FEMALE.— Similar to male except frons wider, broadly convex, carina absent.

TYPE MATERIAL.— The male holotype (upper), female allotype (middle), and one paratype (bottom), all mounted on one pin, and nine other paratypes were taken at Amarampalam R., Nilambur, Madras, India, IV-1933, from *Tiliacora acuminata*, by C.F.C. Beeson. The holotype, allotype, and one paratype are in the Forest Research Institute, Dehra Dun; nine paratypes are in my collection. Several other specimens bearing these data are in the FRI.

Pityophthorus cedri, n. sp.

Under this name is included *cedri* Beeson, *kashmirensis* Beeson, and *gerardianus* Beeson, all manuscript names that have been cited in the literature. Among Indian species, it is distinguished by the moderately impressed elytral declivity, by the occurrence of a conspicuous median carina on the frons of both sexes, and by the more nearly concentric pronotal asperities. As in most other Indian representatives of the genus, the discal interstriae are impunctate.

FEMALE.— Length 1.7 mm (paratypes 1.4–1.7 mm), 2.6 times as long as wide; color dark reddish brown.

Frons convex, shining, coarsely and closely punctured, subglabrous, with a conspicuous, acute, median carina.

Pronotum and elytral disc about as in *deodara* (Stebbing) except pronotal asperities in less definite concentric rows; pronotal disc more closely, deeply punctured. Elytral declivity distinctly, shallowly sulcate from slightly elevated suture to interstriae 3, 3 armed by three small granules, area between summits on 3 smooth, shining, impunctate. Vestiture of fine, sparse hair, limited to sides and declivity, setae on interstriae 3 rather long.

MALE.— Similar to female except serrations on anterior margin of pronotum and granules on elytral declivity distinctly larger.

TYPE MATERIAL.— The female holotype, male allotype, and two paratypes were taken at Buniyar, Jhelum Valley, Kashmir, India, 21-VI-1928, 5000′, from *Cedrus deodara* twigs, by C.F.C. Beeson; four paratypes are labeled Kilba, U. Bashahr Div., Punjab, India, 26-V-1930, 7000′, *Pinus gerardiana*, H.G. Champion. The holotype and allotype are in the Forest Research Institute, Dehra Dun, and the paratypes are in my collection. Numerous additional specimens in the FRI could not be included in the type series.

Pityophthorus chilgoza, n. sp.

Part of *chilgoza* Beeson, nomen nudum, is this species, part is of *deodara* (Stebbing). This species superficially resembles *deodara*, but it is not closely related. It is distinguished by the long pubescence on the female frons, by the absence of a carina on the female frons, by the less strongly (shallowly) impressed declivital sulcus, and by the much more confused arrangement of smaller pronotal asperities.

Female.— Length 1.4 mm (allotype 1.45 mm), 2.8 times as long as wide; color yellowish brown.

Frons flat from eye to eye, finely, rather closely punctured near margins, ornamented by a marginal fringe of long hair, longest setae equal to about half width of frons, setae in central area sparse to obsolete and much shorter.

Pronotum 1.1 times as long as wide; sides on basal half almost straight and parallel, rather narrowly rounded in front, anterior margin armed by four serrations, median pair much longer; asperities smaller and more strongly confused than in other Indian species; posterior areas smooth, shining, rather finely, not closely punctured. Glabrous except for sparse setae near margins.

Elytra 1.8 times as long as wide; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae not impressed, punctures moderately large, deep; interstriae less than twice as wide as striae, smooth, shining, impunctate. Declivity rather steep, weakly bisulcate; strial punctures minute, interstriae 2 widened, smooth, shining, impunctate, 3 unarmed, a few small punctures evident. Vestiture of minute strial hair and, on declivity, a few short, erect, interstrial setae.

Male.— Similar to female except frons somewhat convex, its surface irregularly punctate-rugose, shining, with a short, acute, median carina, vestiture inconspicuous, fine, short.

Type material.— The female holotype, male allotype, and two paratypes were taken at Kilba, U. Bashahr Div., Punjab, India, 26-V-1930, 7000′, from *Pinus gerardiana*, by H.G. Champion. The holotype and allotype are in the Forest Research Institute, Dehra Dun; the paratypes are in my collection. There are 12 specimens of this species in the FRI that could not be included in the type series.

Pityophthorus glutae, n. sp.

This is the most unique representative of the genus in India. It is distinguished by the larger size, by the strongly impressed elytral declivity, and by the unique female frons as described below.

Female.— Length 1.8 mm (paratypes 1.8–2.1 mm), 3.0 times as long as wide; color yellowish brown.

Frons narrower than usual, flattened to feebly concave from epistoma to vertex from eye to eye, its shining surface closely, rather coarsely punctured, an acute median carina beginning just above epistomal margin and ending near vertex, its greatest height on upper half; vestiture of rather abundant, fine hair of moderate length on impressed area, median third of vertex giving rise to a pencil tuft of very long hair that tends to extend two-thirds of distance toward epistoma and conceal carina.

Pronotum 1.2 times as long as wide; sides almost straight and parallel on more than basal half, broadly rounded in front; anterior margin armed by eight or more low, basally confluent serrations; asperities rather small, numerous, confused; basal areas smooth, shining, with many impressed points and rather sparse, small punctures. Almost glabrous.

Elytra 1.7 times as long as wide; sides almost straight and parallel on more than basal two-thirds, rather narrowly rounded behind; striae not impressed, punctures rather coarse, deep; interstriae only slightly wider than striae, smooth, shining, impunctate. Declivity steep, strongly sulcate; striae 1 and 2 clearly punctured; interstriae 1 distinctly elevated, flat, gradually increasing in width toward apex, with a row of minute punctures and one subapical granule; 2 smooth, shining, impunctate, widest just below middle, 3 strongly elevated and armed by three widely spaced, pointed denticles. Vestiture hairlike, very sparse, on or near declivity.

MALE.— Similar to female except frons broadly convex, without a carina, punctures less abundant, vestiture short, sparse, inconspicuous; serrations on anterior margin of pronotum larger; declivital impression slightly deeper, with two upper tubercles on each side larger, lower one reduced or obsolete.

TYPE MATERIAL.— The female holotype, male allotype, and two paratypes were taken at Tinnevelly, S. Madras, VIII-1925, from *Gluta travancoria*, by D.F.O. Eight paratypes are labeled Evergreens, Tennevelly, Madras, 4-V-1938, R.R.D. 294, B.C.R. 89, cage 500, *Gluta travancoria*, A.H. Khan. The holotype and allotype are in the Forest Research Institute, Dehra Dun, the paratypes in my collection. Several additional specimens are in the FRI and could not be included in the type series.

Scolytogenes indicus, n. sp.

The Schedl Collection in the Wien Museum contained a Schedl note that indicated he had confused *Cryphalomorphus indicus* Beeson, nomen nudum, with his *varius* from New Guinea. However, these species are quite unrelated. This species is smaller, more slender, more finely sculptured, and has stouter setae than does *varius*.

MALE.— Length 1.2 mm (paratypes 1.5–1.9 mm), 2.3 times as long as wide; color very dark brown, pronotum almost black, vestiture pale.

Frons broadly convex, median line above eyes forming a transversely etched, indefinite summit; surface finely rugose-reticulate on upper areas, smoother, roughly, not sharply punctured below, a transverse pair of widely spaced granules near middle; vestiture of fine, rather inconspicuous hair of moderate length. Pronotum 1.0 times as long as wide; widest on basal third, sides moderately arcuate, anterior margin rather broadly rounded; summit near middle, asperities on anterior slope rather coarse; rather finely, closely punctured behind, posterior margins of punctures toward summit slightly elevated to granulate, posterolateral punctures close, only slightly distorted by subgranulation. Vestiture of rather short, recumbent hair.

Elytra 1.2 times as long as wide, 1.3 times as long as pronotum; striae not impressed, except weakly near declivity, punctures rather small, deep, in definite rows except confused on less than basal fourth of disc; interstriae almost twice as wide as striae, punctures near base resembling those of striae (and usually confused with them), their anterior margins elevated toward declivity to form rows of subvulcanate granules (one row on each interstriae). Declivity steep, broadly convex; sculpture about as on disc except interstriae 1 more distinctly impressed, granules on all interstriae larger in diameter but not higher than on disc. Vestiture consisting of very minute strial hair and rows of erect, pointed bristles; each bristle as long as distances between rows, spacing within a row distinctly less, setae stout but not scalelike, apical third of each tapered to a sharp point; a few short supplemental setae on declivity almost scalelike.

FEMALE.— Similar to male except area behind pronotal summit apparently more granulate; small, scalelike setae on elytral declivity more numerous.

TYPE MATERIAL.— The male holotype, female allotype, and two paratypes were taken at Amarkantak, Rewah State, C.I., 1928, 3500′, R.R.D. 783, R.C.R. 144, cage 111, from Burma, by C.F.C. Beeson. The holotype emerged 23-II, allotype 25-II, paratypes 19 and 28-V. Nine paratypes are labeled Mandvi, W. Thana, Bombay 4, 9, or 12-XII-1929, R.R.D. 38, R.C.R. 114, cage 663, *Wrightia tinctoria*, B.M. Bhatia; three paratypes are labeled Gogaldara, Pir Panjal, Kashmir, India, 2-VI-1928, *Hedera helix*, C.F.C. Beeson; three paratypes are labeled Dehra Dun; U.P., India, 7-IV-1931, *Moringa pterygosperma*, M. Bose. The holotype and allotype are in the Forest Research Institute, Dehra Dun; the paratypes are in my collection. Several additional specimens in FRI could not be included in the type series.

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SPECIES COMPOSITION, EMERGENCE, AND HABITAT PREFERENCES OF TRICHOPTERA OF THE SAGEHEN CREEK BASIN, CALIFORNIA, USA

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ABSTRACT.—An extensive study of larvae and adult Trichoptera of the Sagehen Creek basin, Sierra Nevada, California, USA, revealed 77 species representing 14 families and 41 genera. Twenty-six species were restricted to small water bodies (spring sources, seeps, spring streams, temporary ponds, and intermittent streams); 27 were restricted to Sagehen Creek, a second-order stream, and the mouths of two large spring streams. Similarity between species caught at black lights and those in emergence traps was 43%. There were two major peaks in adult emergence by species, midsummer and late summer–fall. A few species emerged during winter or throughout most of the year. The species composition of the community showed affinity with Oregon, the Great Basin, and the Rocky Mountains but very little similarity with the California Coast Range. Four of the most abundant species in the basin have very restricted distributions. Ecological separation of several groups of closely related species could be explained by major differences in larval habitats or by different emergence periods.

Trichoptera from the Sierra Nevada of California have been collected and described in papers over the last several decades, but no comprehensive studies of species abundance and distribution exist for the Sierra Nevada or for any part of it. The Sagehen Creek basin on the east side of the Sierra Nevada has been the site of a University of California field station and of numerous aquatic biology studies since 1951. Trichoptera from this watershed have been critical to several systematic (i.e., Denning 1970, Wiggins 1973, 1977, Parker and Wiggins 1985) and behavioral studies (Erman 1981, 1984, 1986, 1987). Other aquatic invertebrate work in the Sagehen Creek basin is extensive. A comprehensive list of the stoneflies was published by Sheldon and Jewett (1967) and updated by R. Baumann, W. Shepard, B. Stark, and S. Szczytko for the first North American Plecoptera Conference in 1985 (unpublished). Plecoptera material from the Sagehen Creek basin has contributed to many systematic (Jewett 1966, Surdick 1981, Szczytko and Stewart 1979, 1984) and ecological studies (Sheldon 1969, 1972, 1980).

The Turbellaria have been studied (Kenk 1970, 1972) as has the amphipod genus *Stygobromus* (Holsinger 1974); and the *Cricotopus-Nostoc* relationship was first described in Sagehen Creek (Brock 1960). The aquatic invertebrate community and secondary production in peatlands have been examined (Erman and Erman 1975).

The primary objectives of the present study were to determine the species composition, emergence periods, and habitat preferences of the Trichoptera community of the Sagehen Creek basin. As the study progressed, secondary objectives emerged, such as a comparison of collecting methods, development of emergence collection techniques for remote areas, and examination of some taxonomic problems.

STUDY AREA

Sagehen Creek basin is on the east side of the northern Sierra Nevada, Nevada and Sierra counties, California, and on the western edge of the Great Basin in the Lahontan drainage. It includes 2,700 hectares from its headwaters (elevation 2,256 m) to its end in Stampede Reservoir (elevation 1,804 m). Mean annual precipitation is 93 cm, most of which falls as snow. Mean annual temperature at the field station measuring station (1,943 m) is 4.9 C, and temperatures below freezing can occur in any mouth. Within the Sagehen Creek basin is a wide diversity of aquatic habitats. In addition to the second-order, spring-fed Sagehen Creek, there are many permanent, constant-temperature springs (3.5–9 C) and spring streams of various sizes and physical-chemical conditions, several minerotrophic peatlands (fens) in different stages of evolution (Erman 1976, Bartolome et al. in press), a small cirque pond at the head of the basin that dries completely about two out of three years, and temporary streams that exist each year for varying time periods.

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Methods

Adults were collected with emergence traps, black lights, hand nets, and fish traps. Emergence traps were of two types: one, a 1 × 1-m base pyramidal trap with collecting bottle (80% alcohol) that was emptied at one- or two-week intervals; the other, a smaller folding trap that could be easily moved to more remote sites. During the six years of the study over 800 one- or two-week emergence trap samples were collected in 22 locations in the basin, including spring sources, spring streams (first-order streams), an intermittent stream, and Sagehen Creek. Fish traps, used in other studies, were closed screen boxes, open only on the ends. They extended above the water and were emptied from the hinged top (see Erman and Leidy 1975). They were useful for collecting both larval and adult caddisflies. Black lights were used in the vicinity of the U.C. field station. One black light was run intermittently in the same location (about 30 m from the nearest water) at the field station from as early as April to as late as October from 1980 to spring 1987. This light was not a trap; specimens were sampled at approximately half-hour to one-hour intervals on 111 nights. Other portable black lights were used in remote areas. Hand-netting and sweep-netting of vegetation were done at many aquatic sites in the basin.

Larvae were collected with kick screens, Surber-type samplers, and scoops. They were also collected by hand-picking. The objective of the combination of sampling techniques was to collect, if possible, all Trichoptera species in the basin and to determine the larval habitats of all species collected. To that end, many larvae were also reared. Quantitative sampling was not an objective; however, for comparative purposes, the emergence traps provided data on relative abundance of species.

A reference collection of most species will be placed in the California Academy of Sciences, Golden Gate Park, San Francisco. Some of the more rare species and those for which taxonomic questions have yet to be resolved have been or will be sent to the Royal Ontario Museum, Toronto, Canada.

Results and Discussion

Species Habitats and Distribution

A total of 77 species representing 14 families and 41 genera were collected in the basin (Table 1). Limnephilidae was the most abundantly represented family with 32 species, followed by Rhyacophilidae with 13 species. Larval habitats were determined for most species and are given in Table 1. Habitats could not be determined for 12 species caught only by black light and for whom larvae were unknown.

Twenty-six species occurred in one small water body or a combination of spring sources, spring seeps, spring streams, temporary ponds, and intermittent streams but not in Sagehen Creek. At least one-third of the species in the basin, then, were restricted to smaller aquatic habitats. Conversely, at least 27 other species, approximately another one-third, were confined to Sagehen Creek and/or near the mouths of the two largest spring streams only. Twelve species were found in both general habitat groups, though they may have shown a preference for one or the other.

Fifteen species from six families showed a variety of adaptations for life in variable habitats at the land-water interface and are discussed in more detail elsewhere (Erman 1981, 1986, 1987). Larvae of *Clostoeca disjuncta* were never found in permanent water. Adults of *Hesperophylax designatus* and *Wormaldia pachita* emerged from an intermittent stream just days before it dried completely. *Limnephilus peltus* left permanent spring streams and pupated in damp moss; in laboratory rearing studies it could not emerge if left in permanent water. A few species (i.e., *Goeracea oregona*, *Allomyia cidoipes*, *Lepidostoma ermanae*) were limited to one or a few springs. The distribution of the species in springs and their requirements will be discussed further in a future paper, the result of a separate study on Sierra Nevada springs.

Species Abundance

Relative abundance of species given in Table 1 is based roughly (a) on number of adults caught during the study, (b) on distribution in numbers of habitats based on emergence trapping, and (c) on an assessment of larval abundances. The ratings shown are, of necessity, somewhat subjective. The 10 species designated as abundant were either caught in very high numbers at black lights and were present as larvae in large numbers in Sagehen Creek (7 species), or were caught in high numbers in emergence traps and in many locations (3 species). In this latter group, one species, *Desmona bethula*, inhabits newly flooded areas and fluctuates greatly in numbers from year to year (Erman 1981). Thus, it may not always be abundant. Both it and *Limnephilus peltus*, discussed above, have an apparently limited range in the Sierra Nevada but occur, at least periodically, in great abundance in the Sagehen Creek basin (see also Denning 1965).

Thirty-six species are listed here as common, and 31 are considered rare. In the rare group are 2 species that occur in rather high numbers but were found in only one habitat or a few small ones within the basin. These are *Goeracea oregona* (in one spring only) and *Parthina linea* (a few spring areas). *Parthina linea* exhibits an elaborate, nearly flightless mating behavior on riparian vegetation (Erman 1984), which may partly explain its limited distribution. Females may be flightless. Similar behavior has been observed in the limnephilid *Psychoronia costalis* (Scott Herrmann, personal communication), also confined to spring seeps and small streams.

Trapping Success and Differences

Fifty-seven species were caught in emergence traps, and 52 were caught at black lights (Table 1). Thirty-three species were trapped by both methods. Thus, 24 species caught in emergence traps were never caught at black lights, and 19 species caught by black lights were not caught in emergence traps. One species, *Dicosmoecus gilvipes*, was caught only by hand-netting and by larval rearing. These results give a trapping similarity of 43% (using Jaccard's Index, Pielou 1984) between the methods and indicate the value of using different trapping methods to determine total species in a given geographical area.

Most species not caught at black lights were from the springs and spring streams (Table 1) and/or emerged during a season other than summer (Fig. 1). Many factors, such as location of trap in relation to microhabitat of a species, diel flight activity, time of year of emergence, and attraction to light, affect trapping success and could be considered on a species-by-species basis. The objective of this study, however, was not to study reasons for trapping success but to collect all species possible, and no attempt was made to quantify trapping effort for each technique.

Fish traps were considered emergence traps for the foregoing comparison. They accounted for collection of only four species that were not otherwise caught in emergence traps. They may catch caddisflies, however, during up- or downstream flight rather than during emergence.

Adult Flight Periods and Community Emergence Patterns

Emergence periods are shown for each species in Figure 1. Species are listed in order of emergence (and, within that category, alphabetically by family and species) beginning with January. The year was divided into 52 numbered weeks by eliminating 29 February and 31 December, as in the Rothamsted Insect Survey (Crichton 1971). To save space in this paper (Figs. 1, 2), I have begun with week 14 (2–8 April) and ended with week 44 (29 October–4 November). Traps were run, however, at some sites year-round, and the following four species were collected in late autumn, winter, and early spring: *Psychoglypha klamathi*, *P. mazamae*, *P. ormiae*, and *Wormaldia occidea*. The four Sagehen *Psychoglypha* species (including *P. bella*) do not emerge in the summer period. *Wormaldia occidea*, on the other hand, was collected at constant-temperature springs during every month of the year and apparently has a nonseasonal life cycle. *Rhyacophila oreta* began emerging in early February and was collected in every week through September. It had a similar long, nonseasonal emergence period in the Salmon River basin of Idaho (Smith 1968). Four other species (*Desmona bethula*, *Rhyacophila ardala*, *R. vaccua*, and *R. verrula*) were occasionally trapped in November and December.

There are two major peaks in adult emergence in the Sagehen Creek basin Trichoptera community. One is the midsummer peak in late June and July. The other is the late summer–fall peak that begins as the temperature cools in August. At least 20 species in the

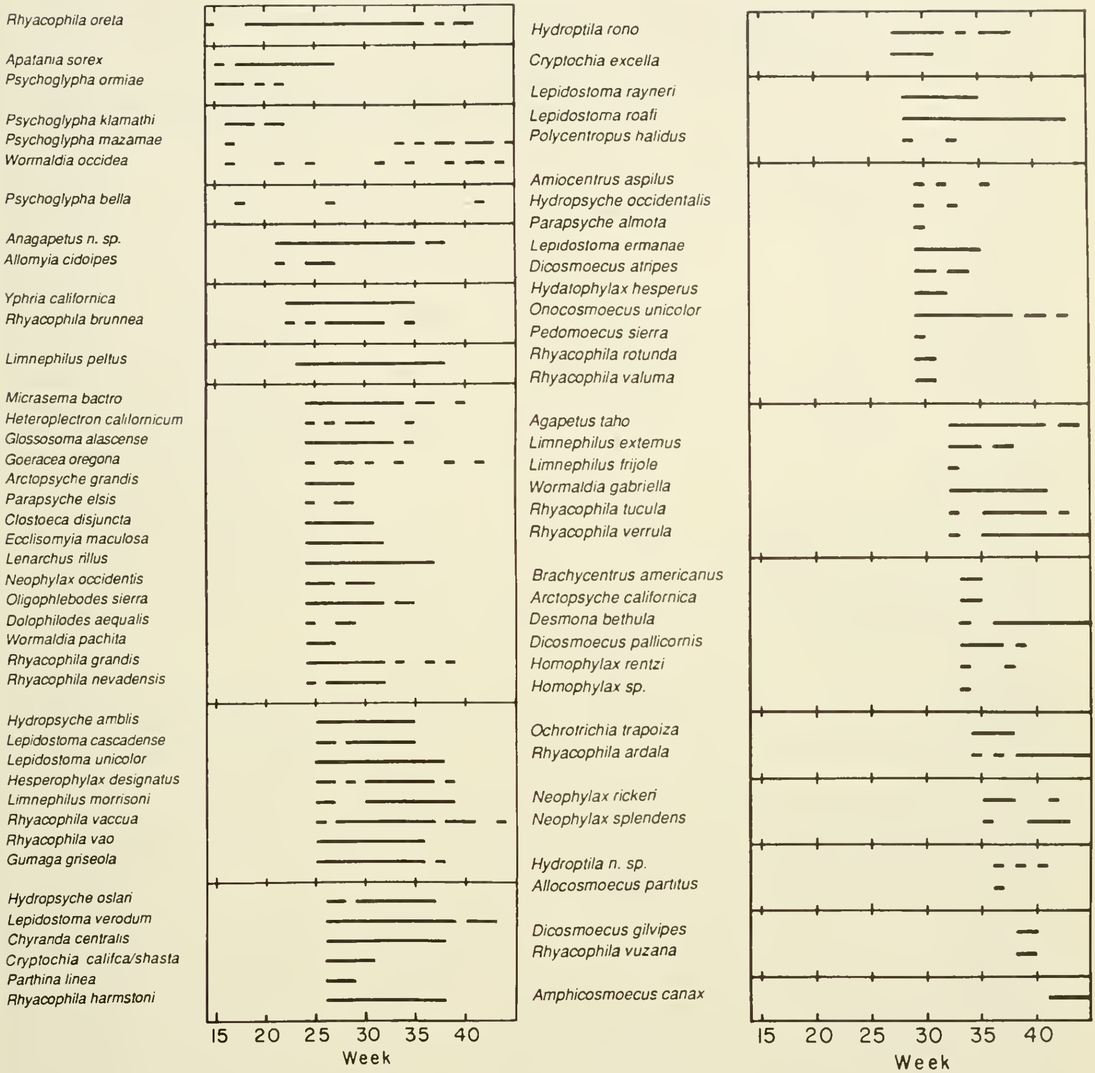

Fig. 1. Adult emergence periods of Trichoptera from the Sagehen Creek basin, by week, 2 April–4 November.

basin are in this latter category. Adult activity patterns for rarely caught species with no larval information must be considered inconclusive. The combined species emergence (Fig. 2) for 1979–1986 shows a pronounced increase in emergence in week 24 (11–17 June). This pattern is plotted against air temperature, water temperature in Sagehen Creek (means from 1979 to 1986), and solar radiation (taken as the mean monthly radiation published for a similar latitude—Reno, Nevada). No correlation is obvious to explain the sudden rise in numbers of emerging species. There is, however, an obvious association between the overall emergence pattern and these three physical factors. The solid bars represent all species in the basin; the open bars, Sagehen Creek species only. It should be remembered that the water temperature curve in Figure 2 does not apply to species living in temporary streams, springs, etc.

Geographical Comparisons

Presence or absence of Sagehen Creek basin species in other geographic areas is

TABLE 1. Species composition, habitat, relative abundance, and capture method for Trichoptera in the Sagehen Creek basin, California. [SC = Sagehen Creek, S = spring origins, SS = spring streams, LSS = largest spring streams only (near mouth), TS = temporary streams, TP = temporary ponds.]

			Capture method		
Species	Habitat	Relative abundance	Emergence trap	Black light	Reared or associated larvae
Brachycentridae					
Amiocentrus aspilus (Ross) 1938	?	R		X	
Brachycentrus americanus (Banks) 1899	SC[1]	R		X	X
Micrasema bactro Ross 1938	SC,S,SS	A	X	X	X
Calamoceratidae					
Heteroplectron californicum McLachlan 1871	SC,LSS	C	X	X	X
Glossosomatidae					
Agapetus taho Ross 1947	SC,LSS	C	X	X	X
Anagapetus sp.	SC,S,SS	A	X	X	X
Glossosoma alascense Banks 1900	SC	A	X	X	X
Goeridae					
Goeracea oregona Denning 1968	S[2]	R[5]	X		X
Hydropsychidae					
Arctopsyche californica Ling 1938	?	R		X	
Arctopsyche grandis (Banks) 1900	SC	C	X	X	X
Hydropsyche amblis Ross 1938	SC,LSS	A	X	X	X
Hydropsyche occidentalis Banks 1900	?	R		X	
Hydropsyche oslari Banks 1905	?	R		X	
Parapsyche almota Ross 1938	LSS	R	X		
Parapsyche elsis Milne 1936	LSS	R	X		
Hydroptilidae					
Hydroptila rono Ross 1941	SC,SS[3]	C	X	X	X
Hydroptila sp.	SC	R	X	X	
Ochrotrichia trapoiza Ross 1947	SS[3]	R	X		
Lepidostomatidae					
Lepidostoma cascadense (Milne) 1936	SC,SS	C	X	X	
Lepidostoma rayneri Ross 1941	?	C		X	
Lepidostoma roafi (Milne) 1936	SC,S,SS	A	X	X	X
Lepidostoma unicolor (Banks) 1911	SC,S,SS	C	X	X	
Lepidostoma verodum Ross 1948	S,SS	C	X		
Lepidostoma ermanae Weaver 1988	S[4]	R	X		X
Limnephilidae					
Allocosmoecus partitus Banks 1943	SC	R		X	X
Allomyia cidoipes (Schmid) 1968	S[4]	R	X		X
Amphicosmoecus canax (Ross) 1947	SC,LSS	C	X		X
Apatania sorex Ross 1941	SC,LSS	C	X		X
Chyranda centralis (Banks) 1900	SC,S,SS	C	X	X	X
Clostoeca disjuncta (Banks) 1914	TS	C	X	X	X
Cryptochia califca/shasta Denning 1968, 1975	SS	R	X		
Cryptochia excella Denning 1964	S,SS	R	X		
Desmona bethula Denning 1954	S,SS,SC	A	X		X
Dicosmoecus atripes (Hagen) 1875	SC,LSS	C		X	X
Dicosmoecus gilvipes (Hagen) 1875	SC[1]	C			X

shown in Table 2. Comparisons were made with published, comprehensive Trichoptera lists from the state of Oregon, from the H. J. Andrews Forest in the western Cascades of Oregon, from Utah, Colorado, southeast Alaska, the Yukon, and from two Pacific Coast Range streams in California (Anderson 1976, Anderson et al. 1982, Baumann and Unzicker 1981, Herrmann et al. 1986, Vineyard 1982, Nimmo and Wickstrom 1984, McElravy and Resh 1987). No attempt was made here to show total range of each species. The purpose is to show where the Sagehen Creek basin Trichoptera community has affinities with other western North America Trichoptera, which Sagehen Creek basin species are widely

Table 1 continued.

Species	Habitat	Relative abundance	Capture method		Reared or associated larvae
			Emergence trap	Black light	
Dicosmoecus pallicornis Banks 1943	?	C		X	
Ecclisomyia maculosa Banks 1920	SC, LSS	C	X	X	X
Hesperophylax designatus Banks 1943	TS, S, SS	C	X		X
Homophylax rentzi Denning 1964	S^4	R		X	
Homophylax sp.	S	R	X		
Hydatophylax hesperus (Banks) 1914	?	R		X	
Lenarchus rillus (Milne) 1935	TS, TP, S, SS	C	X	X	X
Limnephilus externus Hagen 1861	TP	C		X	X
Limnephilus frijole Ross 1944	?	R		X	
Limnephilus morrisoni Banks 1920	TS, SS	C	X	X	X
Limnephilus peltus Denning 1962	S, SS	A	X	X	X
Neophylax occidentis Banks 1924	SC	C	X	X	X
Neophylax rickeri Milne 1935	?	R	X	X	
Neophylax splendens Denning 1948	S, SS	R	X	X	
Oligophlebodes sierra Ross 1944	SC	A		X	X
Onocosmoecus unicolor Banks 1897	SC, LSS	C	X	X	X
Pedomoecus sierra Ross 1947	?	R		X	
Psychoglypha bella (Banks) 1903	SC	C		X	X
Psychoglypha klamathi Denning 1970	SS	R		X	
Psychoglypha mazamae Denning 1970	S, SS	C	X		X
Psychoglypha ormiae (Ross) 1938	S	R	X		
Odontoceridae					
Parthina linea Denning 1954	S^2, SS	R^5	X		X
Philopotamidae					
Dolophilodes aequalis (Banks) 1924	SC	R	X	X	X
Wormaldia gabriella (Banks) 1930	SC, LSS	C	X	X	
Wormaldia occidea (Ross) 1938	S	C	X		
Wormaldia pachita Denning 1956	TS	R	X		
Phryganeidae					
Yphria californica (Banks) 1970	SC, S^2, SS	C	X	X	X
Polycentropodidae					
Polycentropus halidus Milne 1936	SC	R	X		
Rhyacophilidae					
Rhyacophila ardala Denning 1965	S, SS	A	X		X
Rhyacophila brunnea Banks 1911	SC, LSS, S^2	C	X	X	X^6
Rhyacophila grandis Banks 1911	S, SS	C	X	X	X
Rhyacophila harmstoni Ross 1944	SC, S, SS	A	X	X	X
Rhyacophila nevadensis Banks 1924	SC	C	X	X	X
Rhyacophila oreta Ross 1941	S	C	X		X
Rhyacophila rotunda Banks 1924	?	R		X	
Rhyacophila tucula Ross 1950	SC, LSS	C	X	X	X
Rhyacophila vaccua Milne 1936	SC, S, SS	C	X	X	X
Rhyacophila valuma Milne 1936	?	R		X	
Rhyacophila vao Milne 1936	SC, LSS	C	X	X	X^6
Rhyacophila verrula Milne 1936	S, SS	C	X		X
Rhyacophila vuzana Milne 1936	SC	R	X		X
Sericostomatidae					
Gumaga griseola (McLachlan) 1871	S^2, SS^3, SC	C	X	X	X

[1] Lower Sagehen Creek only.

[2] Warmest (9 C) springs only.

[3] Warmest stretches of spring streams only (max. temp. approx. 27 C).

[4] Coldest springs (approx. 3.5–4.5 C).

[5] Habitat restricted but species abundant in that habitat.

[6] Cannot distinguish *R. vao* larvae from *R. brunnea* larvae.

distributed, and which are restricted in range.

In comparing the Sagehen Creek basin species with other areas, I have considered the following species synonyms based on recently published papers: *Lepidostoma mira* is a synonym of *L. cascadense* (Weaver 1988), *Hesperophylax incisus* is a synonym of *H. designatus* (Parker and Wiggins 1985), *Rhyacophila acropedes* is a synonym of *R. brunnea* (Smith and Manuel 1984).

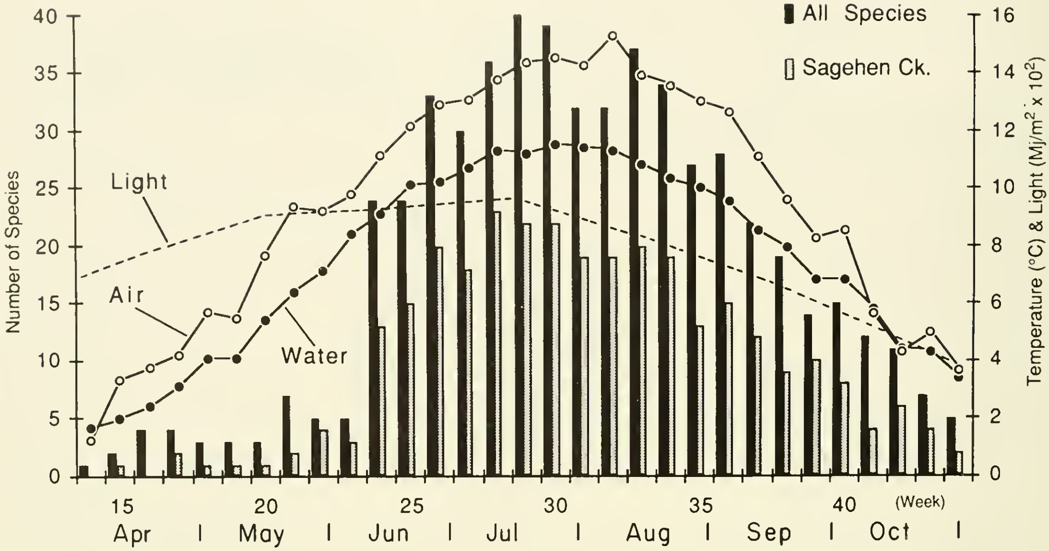

Fig. 2. Weekly emergence of caddisflies from all habitats in the Sagehen Creek basin and from Sagehen Creek only. Air and water temperatures (Sagehen Creek) are weekly means; light is monthly mean solar radiation taken from the nearest recorded site of similar latitude (Reno, Nevada).

Fifty-nine Sagehen Creek basin species are also in Oregon; 36 of these in the western Cascades of Oregon. Thirty-eight species are in common with Utah, 33 with Colorado, 18 with southeast Alaska, 15 with the Yukon, and only 8 with the Pacific Coast Range in California. This latter result may at first seem surprising, except that the California Coast Range has a Mediterranean climate (McElravy and Resh 1987) very different from the short growing season and long, cold winters of the eastern Sierra Nevada. It is apparent that certain species are ubiquitous in western North America (i.e., *Hydropsyche oslari*, *Polycentropus halidus*, *Rhyacophila vao*), and others are probably confined to a small area in the Sierra Nevada. Fifteen Sagehen Creek basin species are found on none of the above regional lists. Of these locally distributed species, it is interesting to note that 4 are among the 10 most abundant species in the Sagehen Creek basin (*Anagapetus* n. sp., *Desmona bethula*, *Limnephilus peltus*, and *Rhyacophila ardala*).

Three species (*Ochrotrichia trapoiza*, *Rhyacophila harmstoni*, and *R. rotunda*) have a wide distribution to the east (Utah and/or Colorado) but not northward. Of course, more extensive collections in eastern Oregon may prove otherwise. Except for those three, all Sagehen Creek basin species found as far east as Utah or Colorado are also found in Oregon.

Hesperophylax magnus was collected from Sagehen Creek on 8 October 1966 (Parker and Wiggins 1985), but it was not collected during the present study. Its earlier presence in Sagehen Creek was the only California site reported and was the westernmost extension of its distribution.

Taxonomic Considerations

Some of the Sagehen Creek basin species show slight variations from described forms; a few are apparently undescribed species for which descriptions are planned.

Anagapetus sp. is an undescribed species similar to *A. chandleri* and *A. aisha*, but it differs from both in a consistent way.

Hydropsyche amblis is the form designated *H. abella* by Denning (1952). I am considering it *H. amblis* here, based on information (Pat Schefter, personal communication) that the species varies widely. My designation is tentative until further work is done.

Lepidostoma ermanae, recently described by Weaver (1988), is similar to *L. hoodi* and *L. spicatum*.

Clostoeca disjuncta differs somewhat in both larva and adult from those described.

The larva has a sclerite on the lateral hump of abdominal segment 1, unlike that described by Wiggins (1977), and makes a case of sedge pieces. The adult has a prominently marked wing. The species shows wide variation over its range (Glenn Wiggins, personal communication).

The few specimens of *Cryptochia califca/shasta* from the Sagehen Creek basin have characteristics of both species. They were all caught in one spring stream over a span of a few weeks. Further work is underway to collect more specimens by emergence trapping to help resolve the taxonomic questions. Both of these species were originally named from single males (Denning 1968, 1975).

I collected *Ecclisomyia* larvae, but no adults, in very cold springs, 3–4 C, at the head of the basin (elevation 2,408 m). These may be a different species from the *Ecclisomyia maculosa* collected from the larger, warmer streams at a lower elevation (1,943 m).

Neophylax rickeri and *Neophylax splendens* warrant further taxonomic and ecological work in other sites where they occur together and in greater abundance than in the Sagehen Creek basin (only 11 males and 6 females total were caught during this study). The males were difficult to separate, and separating the females was little more than guesswork. The two species have the same emergence period in the Sagehen Creek basin. Anderson and Wold (1972) reported a similar finding in Oregon where the two species appeared in the same emergence traps during the same interval in October. *Neophylax splendens* may be a synonym of *N. rickeri.*

A similar situation is true for *Rhyacophila brunnea* and *R. vao.* These species are already known to vary widely (Smith and Manual 1984). Three distinct forms were found during this study, two variants of *R. brunnea* and one of *R. vao.* A few specimens seemed intermediate between the two species. Both species were collected in the same emergence traps at the same time and in the same sweep nets. I have separated the males but think they very likely may be one highly variable species.

Ecological Separation of Some Closely Related Species

Some closely related species in the Sagehen Creek basin, like the three species of *Wormaldia*, occur in completely different aquatic habitats. *Wormaldia pachita* was found in one temporary stream where it emerged just prior to the complete drying of the stream. *Wormaldia occidea*, on the other hand, occurs in constant-temperature springs and emerges year-round. And *W. gabriella* lives in Sagehen Creek and large spring streams only.

Other related species were found in the same habitat but were ecologically separated by the timing of their life cycles. *Agapetus taho*, *Anagapetus* sp., and *Glossosoma alascense*, with similar larvae, all occur in Sagehen Creek but are separated by emergence periods. *Anagapetus* sp. emerges primarily in early summer, *G. alascense* in midsummer, and *A. taho* in late summer and fall. In addition, *A.* sp. is adapted to large and small spring streams as well as Sagehen Creek; *G. alascense* is restricted to Sagehen Creek (Table 1). Other species of these three genera often occur in the same streams (Anderson and Wold 1972).

It is interesting that so many Dicosmoecinae are found in the Sagehen Creek basin, including the three possible species of *Dicosmoecus* and the closely related *Allocosmoecus.* None of these four species was caught in emergence traps, but larval rearings showed that, as predicted by Wiggins and Richardson (1982), *D. gilvipes* and *D. atripes* tended not to be at the same site. *Dicosmoecus gilvipes* larvae live farther downstream in more open, warm areas of Sagehen Creek, and adults emerge later than *D. atripes* (Fig. 1). Larvae of *A. partitus* were infrequently found in the same section of Sagehen Creek as *D. atripes*, but the preferred larval habitats of *A. partitus* and *D. pallicornis* are unknown in the Sagehen Creek basin.

The four species of *Psychoglypha* have similar emergence periods, but *P. bella* is restricted to Sagehen Creek and *P. mazamae* (larvae and adults) is found in warmer downstream sections of small spring streams than are the adults of *P. ormiae* and *P. klamathi.* I have not successfully reared or associated with adults the larvae of these latter two and do not know if the larvae can be distinguished from each other.

The habitat differences of *Chyranda centralis* and *Clostoeca disjuncta* are worth noting because of their similar larvae and cases.

TABLE 2. Presence of Trichoptera species of the Sagehen Creek basin in other western North American areas.

Sagehen Creek basin species	Oregon[1]	Western Cascades[2] (Oregon)	Utah[3]	Colorado[4]	Southeast Alaska[5]	Yukon[6]	Coast Range[7] (California)
Brachycentridae							
Amiocentrus aspilus	X	X	X	X			X
Brachycentrus americanus	X	X	X	X			
Micrasema bactro	X	X	X	X	X	X	
Calamoceratidae							
Heteroplectron californicum	X	X					X
Glossosomatidae							
Agapetus taho	X						X
Anagapetus sp.							
Glossosoma alascense	X		X	X	X	X	
Goeridae							
Goeracea oregona	X						
Hydropsychidae							
Arctopsyche californica							
Arctopsyche grandis	X	X	X	X		X	
Hydropsyche amblis	X						
Hydropsyche occidentalis	X		X	X			X
Hydropsyche oslari	X	X	X	X		X	X
Parapsyche almota	X		X	X			X
Parapsyche elsis	X	X	X	X	X	X	
Hydroptilidae							
Hydroptila rono	X		X	X		X	
Hydroptila sp.							
Ochrotrichia trapoiza			X	?			
Lepidostomatidae							
Lepidostoma cascadense	X	X	X	X		X	
Lepidostoma rayneri	X						
Lepidostoma roafi	X	X	X	X	X	X	
Lepidostoma unicolor	X	X	X	X			
Lepidostoma verodum	X	X					
Lepidostoma ermanae							
Limnephilidae							
Allocosmoecus partitus	X	X					
Allomyia cidoipes	X						
Amphicosmoecus canax	X		X	X			
Apatania sorex	X	X	X				
Chyranda centralis	X		X	X	X	X	
Clostoeca disjuncta	X						
Cryptochia califca/shasta							
Cryptochia excella							
Desmona bethula							
Dicosmoecus atripes	X		X	X	X	X	
Dicosmoecus gilvipes	X	X	X	?			
Dicosmoecus pallicornis							
Ecclisomyia maculosa	X	X	X	X			
Hesperophylax designatus	X		X	X			

Though in separate monospecific genera, they are in the same tribe (Stenophylacini) and in the study area can occur in streams that are separated by only a few meters. However, *Clostoeca* is never in a permanent stream and *Chyranda* is never in a temporary one. The upstream movements of *Chyranda* toward cooler water prior to pupation have been documented (Erman 1986). The last instar and pupa of *Clostoeca* are difficult to find. *Clostoeca* may pupate in damp, decaying organic matter as small streams dry. I have observed *Clostoeca* adults flying upstream over dry runs in early summer, presumably to lay eggs, and in late fall I have collected early instars at the same sites. The same habitat separation of

Table 2 continued.

Sagehen Creek Basin species	Oregon[1]	Western Cascades[2] (Oregon)	Utah[3]	Colorado[4]	Southeast Alaska[5]	Yukon[6]	Coast Range[7] (California)
Homophylax rentzi							
Homophylax sp.							
Hydatophylax hesperus	X	X					
Lenarchus rillus	X				X		
Limnephilus externus	X	X	X	X	X	X	
Limnephilus frijole	X			X			
Limnephilus morrisoni	X						
Limnephilus peltus							
Neophylax occidentis	X	X	X				
Neophylax rickeri	X	X			X		
Neophylax splendens	X	X	X	X			
Oligophlebodes sierra	X	X	X	X	X		
Onocosmoecus unicolor	X	X	X	X	X	X	
Pedomoecus sierra	X	X					
Psychoglypha bella	X	X					
Psychoglypha klamathi	X						
Psychoglypha mazamae							
Psychoglypha ormiae	X		X	X			
Odontoceridae							
Parthina linea	X	X					
Philopotamidae							
Dolophilodes aequalis	X		X	X			
Wormaldia gabriella	X	X	X	X		X	
Wormaldia occidea	X						
Wormaldia pachita							
Phryganeidae							
Yphria californica	X						
Polycentropodidae							
Polycentropus halidus	X	X	X	X	X		X
Rhyacophilidae							
Rhyacophila ardala							
Rhyacophila brunnea	X	X	X	X		X	
Rhyacophila grandis	X	X			X		
Rhyacophila harmstoni			X	X			
Rhyacophila nevadensis				?			
Rhyacophila oreta	X	X	X	?			
Rhyacophila rotunda			X	X			
Rhyacophila tucula	X	X			X		
Rhyacophila vaccua	X	X			X		
Rhyacophila valuma	X	X	X	X	X		
Rhyacophila vao	X	X	X	X	X	X	X
Rhyacophila verrula	X	X	X	X	X		
Rhyacophila vuzana	X	X					
Sericostomatidae							
Gumaga griseola	X		X				
Total species in common	59	36	38	33	18	15	8

[1] Anderson 1976
[2] Anderson et al. 1982
[3] Baumann and Unzicker 1981
[4] Herrmann et al. 1986
[5] Vineyard 1982
[6] Nimmo and Wickstrom 1984
[7] McElravy and Resh 1987

larvae of these two genera has been found in the western Sierra Nevada (Rich Bottorff, personal communication).

Most of the Sagehen *Rhyacophila* are in separate taxonomic groups (Ross 1956, Schmid 1970). Ross and Schmid placed *R. grandis* in the same group with *R. brunnea* and *R. vao*, already discussed; Smith, however, separates *R. grandis* on the basis of larval gills (S. D. Smith, Department of Biological Sciences, Central Washington University, Ellensburg, Washington 98926, unpublished

Key to larvae of Nearctic species groups of *Rhyacophila*, available from author). *Rhyacophila ardala* and *R. vaccua* are the only other pair of closely related *Rhyacophila*. They keyed to the same place in Smith's key but could be separated by head length vs. head width and by correlation with adults from emergence traps. It was then apparent that their habitats are different. *Rhycophila ardala* occurred in cold spring sources, and *R. vaccua* was primarily in Sagehen Creek and near mouths of spring streams close to Sagehen Creek.

CONCLUSIONS

Though the eastern Sierra Nevada is dry and has a brief growing season, a wide diversity of small aquatic habitats, both permanent and intermittent, seems to account for a large and diverse Trichoptera community with species adapted to nearly every aquatic possibility. Similar detailed studies in other Sierra Nevada basins on both east and west sides and in eastern Oregon and Nevada are needed to increase our understanding of California Trichoptera communities. It is unfortunate that, although Trichoptera systematists have collected in California for a long time, so little detailed information about caddisfly communities is known for this state. With ever-increasing demands being made on California waters, and recently on the smaller streams and springs of the Sierra Nevada, a great wealth of evolutionary, ecological, and biogeographical information concerning Trichoptera may be lost before it is ever documented.

ACKNOWLEDGMENTS

I thank the late Don Denning, Glenn Wiggins, Pat Schefter, Stamford Smith, and John Weaver for their help with verification of species and resolution of taxonomic questions. I am grateful to the following people for emptying traps at different times during the study: Chris Kellner, Vernon Hawthorne, Mike Yoder-Williams, Joe Thornton, Wayne Spencer, and Lynn Decker. And my thanks to Don Erman for editorial and field assistance. Partial funding was provided by the University of California Water Resources Center, Project UCAL-WRC-W-645.

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INFLUENCE OF SUBSTRATE WATER CONTENT ON NEONATE SIZE IN THE PRAIRIE SKINK, *EUMECES SEPTENTRIONALIS*

Louis A. Somma[1]

Abstract.—The microenvironment of the nest surrounding most reptilian eggs is known to have a strong influence on the growth and development of embryos. This is particularly true of substrate moisture content. The results of this study suggest that neonatal body size (SVL) increases with increasing substrate wetness in the prairie skink, *Eumeces septentrionalis*. These results agree with studies conducted on other species of reptiles. This study is the first to provide evidence for this relationship in a scincid lizard.

The successful development of reptilian eggs is strongly influenced by their surrounding microenvironment (Packard et al. 1977, 1982, Ackerman et al. 1985, Gutzke and Packard 1987, Packard and Packard 1988). Unlike avian eggs, which experience a net loss of water as incubation progresses (Rahn and Ar 1974), the flexible-shelled eggs of many reptiles experience a net gain in water uptake during normal growth and development (Packard et al. 1982, Tracy 1982, Ackerman et al. 1985).

This study determined the influence of substrate water content on the size (SVL) of hatchling prairie skinks, *Eumeces septentrionalis*. The life history of *E. septentrionalis* has been summarized by various authors (Breckenridge 1943, Nelson 1963, Somma 1985, 1987a, 1987b, 1987c). Data presented herein represent measurements obtained from hatchlings that survived a study determining the effects of soil moisture on egg mortality (Somma and Fawcett, in press).

Materials and Methods

During May and June 1984, 18 gravid female *E. septentrionalis* were collected from Douglas and Pawnee counties in eastern Nebraska, USA. The skinks were housed separately in 26 × 16 × 13-cm plastic terraria containing 600 g (dry mass) of loam (42.2% sand, 44.6% silt, 13.0% clay) obtained from a natural nest site in Douglas County. Lamps suspended above the terraria provided a 14L:10D photothermal cycle. Temperature at the substrate surface cycled from 26 C at night to 34 C during the day. (Methods are also detailed in Somma 1987b, 1987c, Somma and Fawcett, in press).

The soil moisture was maintained, using distilled water, within a range of 15–20% by mass in each terrarium. This range was maintained until the skinks oviposited and their eggs were assigned to a treatment group.

The females oviposited 18–30 June in nest cavities constructed in the substrate. The mean clutch size for *E. septentrionalis* in these populations is 10.95 ± 0.85 (range = 4–18) (Somma 1987b). After each female had oviposited her clutch, the eggs were removed, individually candled, and determined to be viable. The eggs were returned to the nest cavities, and the clutches were assigned randomly to one of three soil moisture treatments: (1) dry, 5–10%; (2) medium, 15–20%; (3) wet, 25–30%. The treatment groups contained 71, 76, and 58 eggs, respectively.

Results

Egg mortality within each treatment was high and significantly influenced by substrate water content (Somma and Fawcett, in press), but it compared favorably with prenatal mortality rates found in natural lizard populations (Turner 1977). Emergence of surviving neonates occurred 14–23 July. Incubation time was 20–22 days (dry), 21–22 days (medium), and 23 days (wet). SVL measurement was taken from each neonate. Weights were not obtained because several neonates had already

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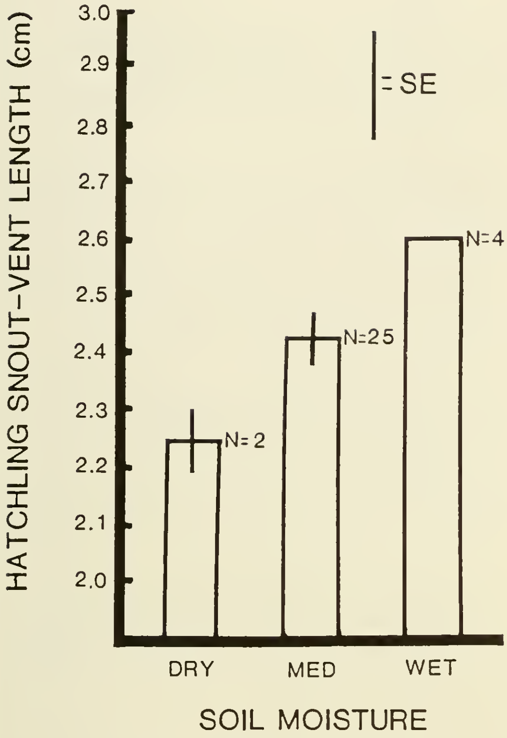

Fig. 1. Effect of substrate water content on neonatal *Eumeces septentrionalis* SVL. Bars represent the means; lines represent ± one standard error of the mean. N = number of neonates. Standard error = 0.00 for the wet treatment.

lost their tails through aggressive interactions with nestmates; these tails were subsequently eaten by the aggressors. A one-way ANOVA (Sokal and Rohlf 1981) of the effect of substrate moisture content on mean neonate SVL was highly significant (F = 18.58, corrected df = 30, $P < .0002$) (Fig. 1). Neonate SVL in *E. septentrionalis* increases with an increase in substrate water content (Fig. 1).

DISCUSSION

The substrate water content is currently recognized as a critical factor in limiting the development and successful hatching of flexible-shelled reptile eggs (Packard et al. 1982, Packard and Packard 1988). Research indicates that water exchange may occur through (1) liquid water exchange between the eggshell and the substrate and (2) water vapor exchange between eggshell and the nest atmosphere (Muth 1981, Packard et al. 1982, Ackerman et al. 1985, Thompson 1987). The results of this study compare favorably with others demonstrating that eggs incubated on successively wetter substrates give rise to larger hatchlings in turtles (Packard et al. 1982, Morris et al. 1983), snakes (Black et al. 1984, Gutzke and Packard 1987), and iguanid lizards (Gordon 1960, Packard et al. 1982, Tracy and Snell 1985). These data are the first to suggest this effect on neonate scincid lizards. Further studies utilizing larger sample sizes are required to more clearly demonstrate this effect.

ACKNOWLEDGMENTS

I sincerely thank J. D. Fawcett for his guidance and helpful suggestions. I thank A. Antlfinger and J. French for their statistical advice. I am grateful to T. Bragg and D. Lewis for their advice on measuring and maintaining soil moisture. T. Cherney, F. Kock, J. Lokke, J. O'Hare, R. Vaughn, L. Ward, and S. Wurster assisted in collecting lizards used in this study. B. K. McNab provided helpful criticism of an earlier version of this manuscript. The soil used in this study was classified by F. Sodek, Department of Soil Science, University of Florida. Funding for this study was provided by the Department of Biology, University of Nebraska at Omaha. The results of this study were part of a master's thesis submitted to the Department of Biology.

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REVIEW OF SELENIUM IN SOILS, PLANTS, AND ANIMALS IN NEVADA

Stephen C. Poole[1], Verle R. Bohman[2], and James A. Young[3]

ABSTRACT.—Selenium is critical in livestock nutrition; forage can be either potentially deficient or toxic in this element. Selenium is accumulated in excessive amounts by a relatively few species of plants. Several of these plants, termed indicator species, occur in the western Great Basin; however, selenium toxicity is not a problem in Nevada for domestic livestock. The detection of marginal dietary deficiencies of selenium is of much greater economic importance to the livestock industry than an excess of this element.

Selenium occurs as a trace element in the composition of various minerals. Selenium levels are very low in volcanic rocks of recent origin. Accumulations of this element require concentration through secondary dispersion and subsequent sedimentation. Therefore, excesses of selenium are usually associated with siltstone, sandstone, or other sedimentary rocks.

Selenium is usually found in soils as selenate, a water-soluble mineral. The selenium concentration of plants is directly related to the selenate concentration in soil. In soils low in selenate, the ability of plants to accumulate selenium is similar. In soils with high levels of selenate, indicator species accumulate 10 times as much selenium as other species. The foliage of most indicator plants is generally avoided by grazing animals. Deficiencies in dietary selenium are associated with the occurrence of white muscle disease, retained placentas, and general unthriftiness of animals. Insufficient dietary selenium can be overcome through injection, intraruminal pellets, or supplementation with salt mixtures.

The biological significance of selenium in animal nutrition was not recognized until 1934, when it was identified as a toxic element that caused lameness and death in livestock grazing certain range plants in the Dakotas and Wyoming (Franke 1934). Although toxic levels of selenium for livestock were first described, deficiencies of dietary selenium are much more widespread. The geographical areas of selenium-responsive diseases have been described in the United States in general (Fig. 1), but specific information on Nevada conditions is fragmentary. Because the geology of Nevada is complex, the relationships between critical plant selenium levels and various geological formations are difficult to define.

GEOBOTANY OF SELENIUM

Selenium can be found in minute amounts in virtually all materials of the earth's crust. Shales, which are sedimentary rocks, have been associated with the majority of selenium-toxic soils, whereas igneous rocks are inherently low in selenium and thus produce selenium-deficient soils. Among the shales, those containing organic matter are the richest in selenium. Selenium can also occur in limestones or sandstones (Fleming 1980). The concentration of selenium in basaltic, granitic, and sandstone rocks averages 0.05 ppm; shales, 0.6 ppm; and carbonate sedimentary rocks, 0.08 ppm (Tarekian and Wedepohl 1961).

Selenium in Rock Formations

Seleniferous geological formations in North America belong to seven different geological periods of time. They include the Tertiary, Cretaceous, Jurassic, Triassic, Permian, Pennsylvanian, and Mississippian periods (Rosenfeld and Beath 1964). The oldest rocks associated with accumulations of selenium are mainly marine limestones, sandstones, and shales from the Mississippian and Pennsylvanian periods of the Paleozoic era. In Nevada, isolated blocks of these very old strata occur in the Schell Creek and Fish Creek ranges of central and eastern Nevada. Sedimentary rocks in these formations derived from sediments with high organic matter content give the highest levels of selenium (Desborough et al. 1979).

Rocks of Triassic age in most parts of the western United States are characterized by

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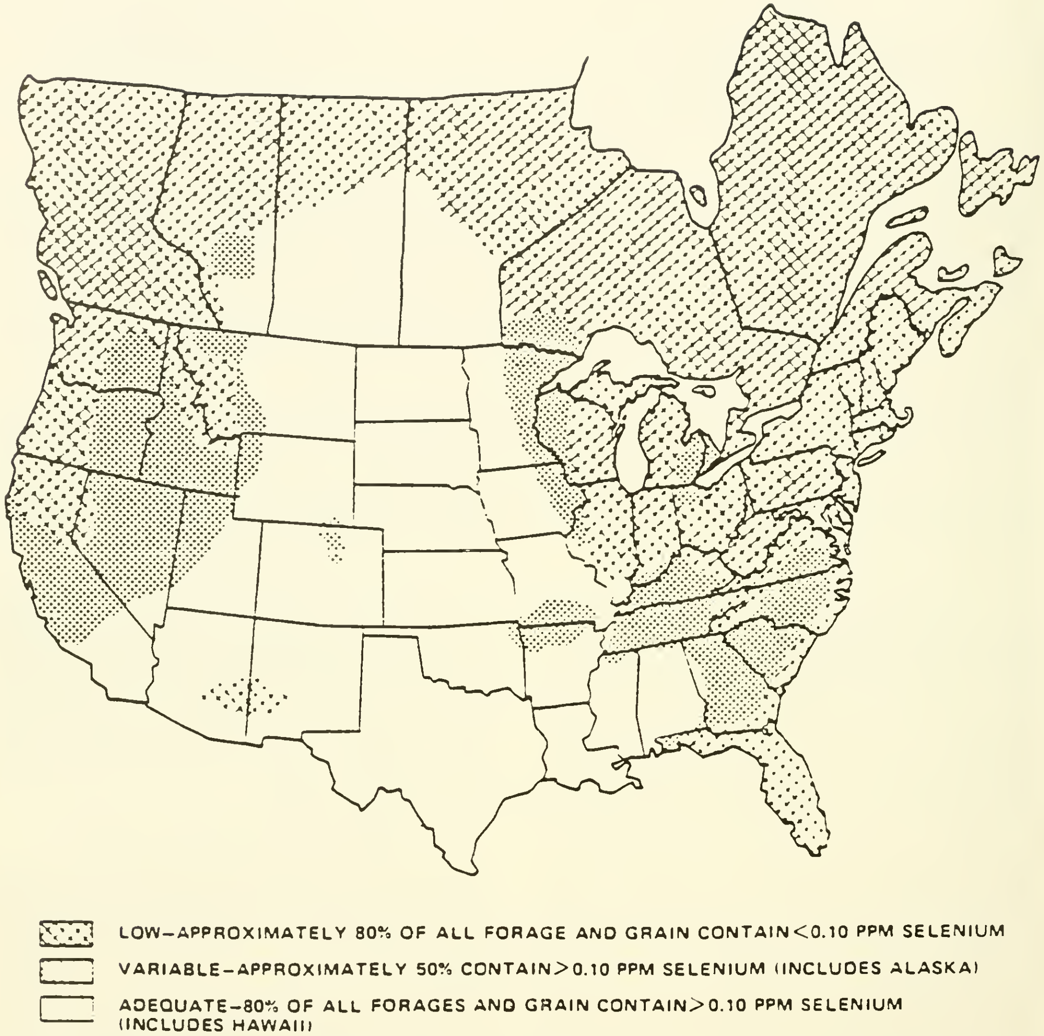
LOW–APPROXIMATELY 80% OF ALL FORAGE AND GRAIN CONTAIN<0.10 PPM SELENIUM
VARIABLE–APPROXIMATELY 50% CONTAIN>0.10 PPM SELENIUM (INCLUDES ALASKA)
ADEQUATE–80% OF ALL FORAGES AND GRAIN CONTAIN>0.10 PPM SELENIUM (INCLUDES HAWAII)

Fig. 1. Selenium content of forages and grains in the United States and Canada as related to mineral nutritional needs of animals. Map from NRC (1983).

their red and brown colors. They are mainly of continental origin and include conglomerates, sandstones, sandy shales, limestones, evaporites, and volcanic or pyroclastic rocks. Triassic strata are identified from New Mexico, Texas, Arizona, Utah, southeastern Idaho, Wyoming, Montana, Colorado, and Nevada (Table 1). The Moenkopi Formation, a lower Triassic formation, is exposed in southeastern Nevada, southern Utah, northern Arizona, and southwestern Colorado. This formation is known to support a variety of seleniferous plants. In fact, most vegetation on the Moenkopi is considered to be high in selenium and hazardous to livestock. The Chinle Formation, an upper Triassic formation, is exposed in northern Arizona, southern Utah, northwestern Colorado, northern New Mexico, and southeastern Nevada. Extensive and varied selenium indicator plants grow on the Chinle Formation. Although plants found on this formation generally contain less selenium than plants from the Moenkopi Formation, their widespread distribution makes them a serious hazard to livestock (Rosenfeld and Beath 1964).

Table 1. Selenium-bearing formations in Nevada[a].

Formation	Period or era	Millions of years ago (approx.)	Nevada location (approx.)
Humboldt	Miocene	2.5–6.8	North of Wells
Chinle	Triassic	205–230	Near Las Vegas
Moenkopi	Triassic	205–230	Near Las Vegas
Phosphoria	Permian	230–285	N.E. Nevada
Unnamed	(Carboniferous)	280	Goose Creek
Unnamed	(Carboniferous)	280	Taylor Canyon
Unknown	Pennsylvanian	285–325	Near Las Vegas
Unnamed	Mississippian	325–350	Round Mountain
Chainman	Mississippian	325–350	Near Ely
Woodruff	Devonian	350–410	Near Ely
Comus	Ordovician	430–500	Near Winnemucca
Unnamed	Paleozoic era	230–600	Near Eureka
Vinini	Ordovician	430–500	Near Eureka

[a] Compiled from Beath et al. (1939), Davidson and Lakin (1961), Rosenfeld and Beath (1964), Tagg (1964), Desborough et al (1979), Poole et al. (1979), and USGS (1975).

Rocks of Pennsylvanian age in the western interior of the United States that contain selenium are mainly marine limestones, sandstones, and shales. Several species of *Astragalus* were collected in southeastern Nevada from an unknown detritus limestone mass believed to be of Pennsylvanian age (Beath et al. 1939).

Tertiary rocks are widely distributed in the western interior of the United States. They are nonmarine, somewhat consolidated deposits of reworked debris from older rocks plus volcanic rocks such as tuffs and lava flows. The Humboldt Formation (Tertiary) is known to support seleniferous *Stanleya*. The Humboldt Formation extends in patches from the west base of the Wasatch Mountains in Utah to the Humboldt River and Humboldt Mountains in northern Nevada (Beath et al. 1939). This formation was originally cited as being of the Pliocene epoch. However, later correlation of the stratigraphic units in the Great Basin assigns the Humboldt Formation to the Miocene epoch (Sharp 1939, Allen 1973).

In the Schell Creek Range in eastern Nevada, samples of the Chainman shale (Mississippian) are relatively high in selenium. Samples from an unnamed Paleozoic formation exposed in the Fish Creek Range near Eureka were also high in selenium (Davidson and Lakin 1961). The Woodruff Formation (Devonian) in the southern Fish Creek Range in Eureka County has been evaluated for several constituents including selenium. The organic matter in this formation was found to contain selenium (Desborough et al. 1979) (Fig. 2).

Phosphate rock samples from the western phosphate field, which covers western Wyoming, northern Utah, northeastern Nevada, southeastern and south central Idaho, and southwestern Montana, contained 1.4–178 ppm selenium (Robbins and Carter 1970). In the West, the rock occurs as marine sedimentary deposits that are considered to be lateral equivalents of the Phosphoria Formation (Tagg 1964).

Other Ordovician and Devonian age marine strata sampled in Nevada have been found to contain anomalously high concentrations of selenium, ranging from 0.2 to 360 ppm, with an average of 32 ppm (Poole et al. 1979). Generally, old rocks of sedimentary origin produce higher concentrations of selenium, and, consequently, selenium indicator plants are generally present. Conversely, rocks of relatively recent origin (Tertiary period), such as the extensive basalt flows of the Pacific Northwest extending into northwestern Nevada, are relatively low in selenium.

Selenium is also concentrated in deposits of minerals left by geothermal water. Selenium is common in epithermal silver-gold, vanadium, and antimony deposits but less common in gold-silver and mercury deposits and is reported to be present in at least 22 ore deposits in Nevada (Luttrell 1959, Davidson 1960, 1964).

Selenium in Soil

The presence or absence of selenium in any soil is dependent upon the interaction of several factors: (1) the presence of selenium in the

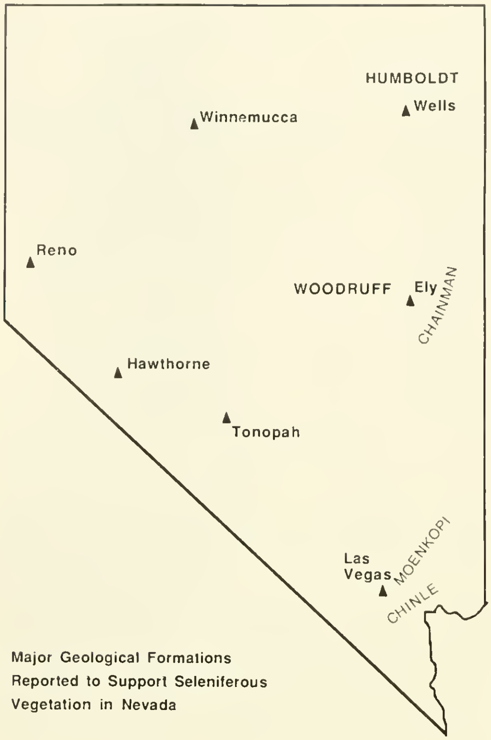

Fig. 2. Major geological formations reported that support seleniferous vegetation in Nevada. These formations are limited to the eastern part of the state. Map compiled from Beath et al. (1939), Sharp (1939), Clark (1957), Davidson and Lakin (1961), Desborough et al. (1979), and Rosenfeld and Beath (1964).

soil parent material, (2) its removal or addition by ground water during soil formation, or (3) its removal or addition by processes subsequent to the formation of the soil (Lakin and Davidson 1967).

Selenium in soil can be found as selenides, selenates, selenites, organic selenium compounds, and, rarely, elemental selenium. The forms and concentration of selenium in a soil solution are determined by various physical-chemical factors expressed as pH, dissociation constants, solubility products, and redox potentials (Geering et al. 1968, National Research Council 1983).

Elemental selenium in soil is readily formed by reduction of selenites in an acid solution. Hydrous oxide complexes of selenites have been recognized as an important form of selenium in acidic soils. The low solubility of selenite complexes may be responsible for the nontoxic levels of selenium in plants growing on acid ferruginous soils high in total selenium. Insoluble selenides associated with sulfides may be present in some soils. The low solubility of the metal selenides, particularly copper selenides, may be responsible for the persistence of selenides in agricultural soils. In well-aerated alkaline soils, other forms of selenium will be oxidized to selenates. Selenates are the primary water-soluble form of selenium in the soil. The selenium content of crop and indicator plants is directly related to the selenate concentration in the soil solution (van Doorst and Peterson 1984).

Recent volcanic deposits, which are inherently low in selenium, constitute the principal soil-forming materials in western Washington, Oregon, northern California, and extreme western Nevada. Parent materials for the soils in extreme northwestern Nevada include igneous and metamorphic rocks along with volcanic ash and sand (USDA 1983). The low-selenium soils are apparently responsible for the low selenium content of the plants grown in this area and therefore the selenium-deficiency symptoms in livestock raised on native forage crops (Allaway et al. 1967, National Research Council 1983). This area of low selenium has as its southern boundary a line extending from the Carson River valley in Nevada northwest across the Sierras and the Sacramento River valley to the Pacific Ocean near Eureka, California. From the Carson Valley, the eastern boundary of the low-selenium area extends north to Lakeview, Oregon, northwest to the Deschutes River valley of Oregon, and then northward parallel with the eastern border of the Cascade Mountains (Kubota et al. 1967). Soils from low-selenium areas in the United States contain less than 0.5 ppm selenium (National Research Council 1983).

On Quaternary period or very recent landscapes where there is a mixture of old sedimentary and recent igneous rocks exposed, the distribution of selenium can be quite complex. Northern Nevada illustrates one of these selenium-variable areas.

Selenium-variable areas within Nevada include many closed basins filled with alluvium and lacustrine sediments interspersed with mountain ranges of volcanic, granitic, and sedimentary rocks. Most of the soils are neutral

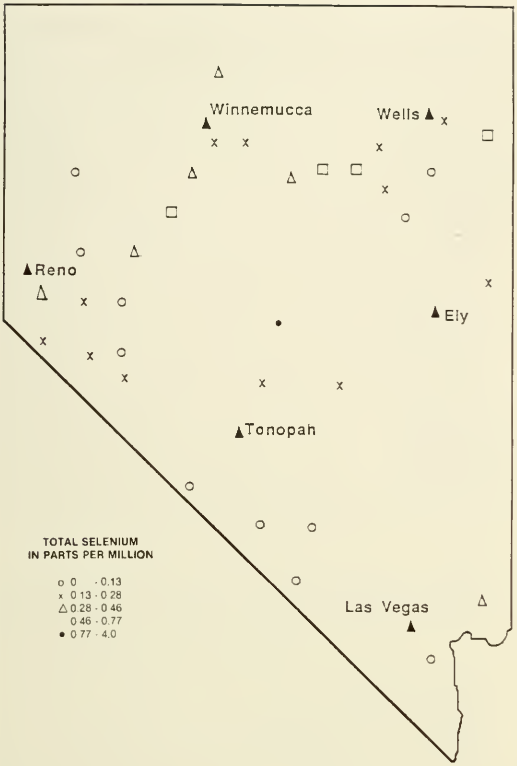

Fig. 3. Total selenium in Nevada soils. Map from Shacklette et al. (1974).

or alkaline, but some acid soils are present in the mountainous areas. The distribution of selenium has several origins: (1) Eocene- and Miocene-aged sediments high in selenium are exposed in scattered areas. (2) Ancient Lakes Bonneville and Lahontan, which once covered much of the intermountain basin area, may have been the recipients of runoff waters from seleniferous areas near their eastern boundaries. (3) Erosion of seleniferous epithermal deposits, scattered throughout Nevada, has contributed selenium to nearby soil materials (Kubota et al. 1967).

A limited survey of Nevada soils as part of a trace element survey of soils throughout the United States revealed a variety of selenium levels (Shacklette et al. 1974) (Fig. 3). Samples were taken at depth of 20 cm below the surface of the deposit to include parts of the zone of alluviation below the plow zone (Shacklette et al. 1971).

Selected trace elements, including selenium, were evaluated in a recently formed alluvial soil (Aquic Xerofluvent) sampled in Nevada. Total selenium levels decreased with increased depth. A total selenium concentration of 0.32 ppm was found in the soil at a depth of 0–61 cm, 0.28 ppm at 64–79 cm, and 0.23 ppm at 79–104 cm (Kubota 1972). Soil samples from central Nevada, along the border of Eureka/Lander counties have been found to contain 0.23–0.28 ppm extractable selenium, primarily as selenate. Soils were of a silt to gravelly loam texture. These soils supported crested wheatgrass (*Agropyron desertorum*) that contained 0.13–0.17 ppm selenium (dry basis) (Poole 1988).

SELENIUM IN PLANTS

Selenium is not known to be essential for plant growth; however, nearly all plants growing on soils containing selenium in a water-soluble available form will absorb, metabolize, and store variable quantities of selenium in their tissues (Hamilton and Beath 1963). The type of plant, its geographical location, and the presence and availability of the element in the soil will influence the selenium content of the plant.

The selenium content in different parts of the plant will vary with the stage of development, the species, and the regrowth of certain species. The differences among plant species in their ability to accumulate selenium from soils low in selenium are relatively small. This is in contrast to selenium accumulation from soils high in selenium in which species differences of tenfold or more are common (Ehlig et al. 1968).

For herbivores, the concentrations of selenium in grazed plants is a useful measure of the nutritional adequacy of their diets. The requirement for selenium is listed as 0.1 mg/kg (ppm) for most domestic animals (Maynard et al. 1979) that subsist almost exclusively on grazed forage.

Forage Plants

Forage plants usually absorb too little selenium to be considered toxic. The levels of selenium in grasses have been found to be only a few parts per million (Shrift 1973). In the United States, extensive areas exist where nearly all plants contain low levels of selenium, such as in the Pacific Northwest, the Northeast, and the Southeastern Seaboard.

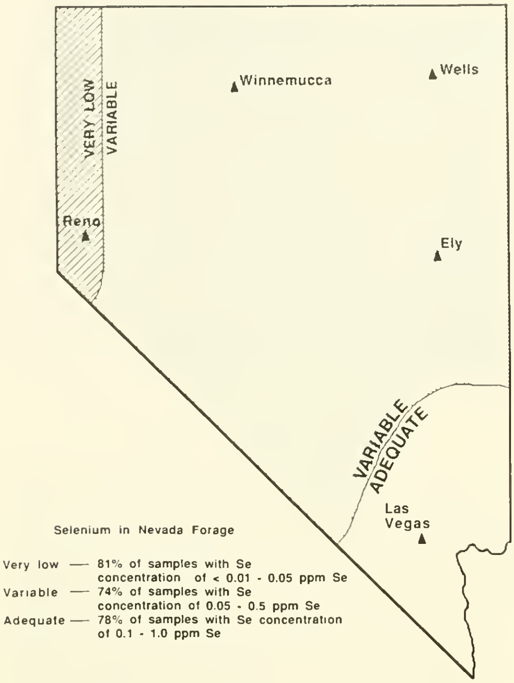
VERY LOW
VARIABLE
Winnemucca
Wells
Reno
Ely
VARIABLE
ADEQUATE
Las Vegas
Selenium in Nevada Forage
Very low — 81% of samples with Se concentration of < 0.01 - 0.05 ppm Se
Variable — 74% of samples with Se concentration of 0.05 - 0.5 ppm Se
Adequate — 78% of samples with Se concentration of 0.1 - 1.0 ppm Se

Fig. 4. Selenium in Nevada forage. Map from Kubota et al. (1967).

Soil and plant surveys have indicated a variety of selenium levels across Nevada. Alfalfa (*Medicago sativa*) has been used as the key plant for sampling. Kubota et al. (1967) found that the selenium concentration in crops was adequate in southern Nevada along the western edge of the Colorado River watershed. In this area over 80% of the plant samples collected contained more than 0.1 ppm selenium and would provide animals with adequate amounts of this element (Fig. 4). A selenium-deficient area may exist in high mountain elevations such as those adjacent to the Humboldt River valley (Kubota et al. 1967) in northern Nevada. This may be the result of acid soils at higher elevations.

Very low concentrations of selenium were found in plant samples along the northwestern border of Nevada, extending from the Carson River valley across the Sierra Nevada and northward toward Oregon. This corresponds to the areas with low selenium in the soil and parent material. More than 80% of the forage samples collected in the low-selenium area contained less than 0.05 ppm selenium and would not provide animals with adequate amounts of this element (Kubota et al. 1967).

In general, most of the high northwestern U.S. rangelands produce forage low in selenium. Carter et al. (1968) sampled primarily alfalfa and, where alfalfa was not available, grasses, other legumes, and grass-legume mixtures in the Pacific Northwest, including Nevada. Selenium concentration was variable, with less than 0.10 ppm selenium in 50% of the samples in the northern portion of Nevada. Plants in the extreme northeast corner and the southern part of the state contained adequate selenium, that is, 90% or more of the samples contained more than 0.1 ppm selenium. In a more detailed study (Carter et al. 1970), samples of mixed forage from high-elevation rangelands of extreme northeastern Nevada contained selenium levels below the dietary requirement of livestock. Forages were growing on Idavada volcanics and silicic rocks of volcanic origin. In contrast, lower elevation range forage and hay produced in the same vicinity contained adequate levels of selenium for livestock.

Alfalfa samples collected near Fallon, Nevada, were highly variable but adequate enough in selenium to prevent white muscle disease (0.05–0.17 ppm) (Allaway and Hodgson 1964). Hay samples from the Yerington, Nevada, area contained 0.12 ppm selenium, thus providing animals with adequate amounts of selenium (T. Erquiaga, unpublished data). Crested wheatgrass collected in central Nevada contained 0.13–0.17 ppm selenium (S. C. Poole and V. R. Bohman, unpublished data).

The selenium intake of cattle grazing northern Nevada rangelands could vary greatly during a single year. If indicator plants were grazed on salt desert ranges, plants with potentially toxic levels of selenium would be consumed. Adequate but nontoxic amounts of selenium would be ingested later while grazing big sagebrush (*Artemisia tridentata*)/bunchgrass ranges, and plants deficient in selenium would be the major part of the diet when mountain brush and meadow ranges were grazed in the summer. Gough and Erdman (1983) have established elemental baseline concentrations for big sagebrush (*Artemisia sp.*) in the western United States, including the Great Basin province. Selenium concentrations ranged from 0.1 to 1.1 ppm

TABLE 2. Selenium accumulator plants[a].

Genus	Common name	Family
Primary indicators		
Astragalus	Poisonvetch	Leguminosae
Stanleya	Prince's plume	Cruciferae
Haplopappus	Goldenweed	Compositae
Xylorhiza	Woody aster	Compositae
Secondary indicators		
Aster spp.	Aster	Compositae
Atriplex spp.	Saltbush	Chenopodiaceae
Castilleja spp.	Paintbrush	Scrophulariaceae
Comandra pallida	Bastard toadflax	Santalaceae
Grayia spp.	Hopsage	Chenopodiaceae
Grindelia spp.	Gumweed	Compositae
Gutierrezia spp.	Snakeweed	Compositae
Machaeranthera sp.	Tansy aster	Compositae
Penstemon spp.	Beardtongue	Scrophulariaceae
Haplopappus spp.	Ironweed	Compositae

[a]Compiled from Kingsbury (1964) and Shrift (1973).

(dry basis), with an average of 0.11 ppm, in the areas sampled. There were no significant differences between provinces.

Selenium Indicator and Accumulator Plants

When selenium was implicated as a toxic agent in western range plants, a survey was undertaken during the 1930s and into the 1940s to determine the extent to which range plants would absorb selenium, their geological distribution, and their geological associations. It became apparent that certain plant species were more reliable than others as indicators of selenium toxic regions. Species from four genera of plants, representing three different families, will accumulate high concentrations of selenium when grown on seleniferous soils or seleniferous geological formations. These plants have been classified as primary indicators. The primary indicator plants are milkvetch (*Astragalus*), of the family Leguminosae; woody aster (*Xylorhiza*), of the family Compositae; goldenweed (*Haplopappus*), of the family Compositae; and prince's plume (*Stanleya*), of the family Cruciferae. Other plants will also absorb toxic levels of selenium from seleniferous soils or seleniferous geological formations; however, they are usually found growing on nonseleniferous soil. These plants include 10 genera representing five different families. They are *Aster*, *Grindelia*, *Gutierrezia*, *Haplopappus*, and *Machaeranthera* of the family Compositae; *Atriplex* and *Grayia* of the family Chenopodiaceae; *Castilleja* and *Penstemon* of the family Scrophulariaceae; and *Comandra* of the family Santalaceae. They are classified as secondary indicators (Table 2) (Kingsbury 1964, Shrift 1973).

All selenium indicator plants are perennials with well-developed root systems that absorb selenium continually throughout the life of the plant. Seasonal changes in the selenium content of indicator plants have been reported (Beath et al. 1937, Olson and Moxon 1939, Rosenfeld and Beath 1964). The absorption of selenium by indicator plants will vary widely depending on the genetic capabilities of the species of plant and the chemical environment in the soil. The effect of one ion on the absorption of other ions by higher plants has been demonstrated. A favorable growing season and an abundance of soil moisture are conducive to high selenium absorption by deep-rooted indicator plants (Rosenfeld and Beath 1964).

Selenium indicator plants are quite unpalatable, and as their selenium content increases they may become even less palatable (Olson 1967). Acute selenium intoxication usually occurs as a result of hungry animals grazing indicator plants, particularly the *Astragalus* species. Consumption of selenium indicator plants in limited amounts over periods of weeks or months can result in chronic selenium poisoning of the blind staggers type (James et al. 1983).

Of the 500 species of *Astragalus* in North America, only about 25 appear to be definite

TABLE 3. Primary indicator plants in Nevada[a].

Family and species	Common name
LEGUMINOSAE	
Astragalus	Milkvetch or poisonvetch
Astragalus haydenianus (Gray)	
A. crotalariae (Benth.) (Gray)	
A. pattersoni var. *praelongus* (Sheld) (Jones)	
A. toanus (Jones)	
A. preussii (Gray)	
A. artemisiarum (A. beckwithii)	
CRUCIFERAE	
Stanleya	Prince's plume
Stanleya pinnata (Pursh) (Britt.)	
S. vividiflora (Nutt.)	
S. elata (Jones)	

[a] Compiled from Tidestrom (1925), Lakin and Byers (1941, 1948), and Sargent (1954).

selenium indicators that grow only on seleniferous soils (Shrift 1973). Even when growing on soils in proximity to selenium-accumulating species, these other species are free from selenium or contain very low levels (Trelease and Trelease 1939).

Seleniferous *Astragalus* species have been collected in Elko and White Pine counties in Nevada. Samples from these plants showed relatively high selenium levels (Beath et al. 1939, Beath et al. 1941, Lakin and Byers 1948). *Astragalus artemisiarum* was collected in areas between Indian Springs, Nevada, and Boulder Dam (Lakin and Hermann 1940). *Astragalus* species collected in the vicinity of the Toano Mountain Range in Elko County and the Schell Creek Range in White Pine County, Nevada, were relatively high in selenium. Seleniferous *Astragalus toanus* was sampled near Wendover, Nevada, on carboniferous shale (Beath et al. 1939) (Table 3).

Astragalus toanus is a woody, sparsely leafed plant found on barren, calcareous clay banks, sandy shales, or clay bluffs. Its occurrence is scattered, but extensive colonies are found where selenium-rich soils are available. It is plentiful in northeast and east central Nevada, especially in the upper Humboldt Valley and extending east into northwest Utah, and occasionally westward in Nevada to the Humboldt Sink, the Quinn River, and the lower Walker River and south to the White River in northeast Nye County. *Astragalus preussii* is a coarse, ill-scented plant and is found on alkaline clay flats, talus in canyons, or gravelly or sandy washes. It is confined to selenium-bearing soils derived from sandstone or limestone. It is locally plentiful but rather scattered in southern Nevada. *Astragalus artemisiarum* (*A. beckwithii*) grows on dry hillsides in alkaline gravelly soils of various origins but prefers limestone and is often among big sagebrush or budsage. It is commonly abundant in northeast Nevada, extending south and becoming rarer (Barneby 1964).

Three species of *Stanleya* occur widely throughout Nevada. In general, they are low in selenium. Whether this is due to low soil selenium, genetic characteristics, or environmental factors is not known. In northern Nevada a sample of seleniferous *Stanleya pinnata* was found on rocks assigned to the Humboldt Formation (Tertiary age) (Beath et al. 1939). Seleniferous *Stanleya pinnata* have also been observed growing on alluvium near Mina, in the vicinity of Indian Springs, and on limestone near Las Vegas (Beath et al. 1939, Lakin and Hermann 1940). *Stanleya pinnata* occurs in diverse numbers of habitats in the upper salt desert and lower *Artemisia* zones in the Lahontan Basin, though it may not be obligatorily bound to seleniferous soils. Other *Stanleya* species have been sampled in the Clark County, Nevada, area and were found to be relatively low in selenium. It would appear that the distribution of seleniferous plants in Clark County is restricted to localized areas (Lakin and Byers 1948).

Extensive and varied species of selenium indicator plants can be found in the southeastern part of Nevada on rock formations of the Upper Triassic period. Seleniferous vegetation has been found near Reno and areas extending south (Rosenfeld and Beath 1964) (Fig. 5).

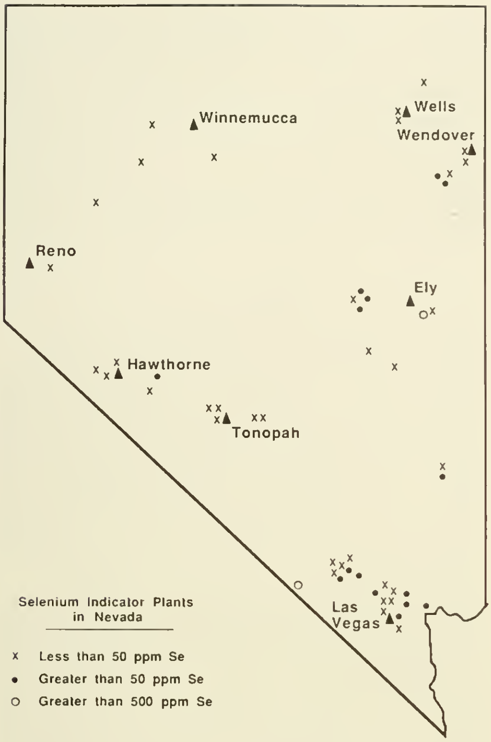

Fig. 5. Selenium indicator plants in Nevada. Map compiled from Beath et al. (1939), Lakin and Byers (1941), Lakin and Hermann (1940), Lakin and Byers (1948), and Rosenfeld and Beath (1964).

NUTRITIONAL SIGNIFICANCE OF SELENIUM IN ANIMALS

Selenium occurs normally in very small amounts in all of the cells and tissues of the animal body and is organically bound (Schwartz 1961, Underwood 1977). Minute amounts of selenium in the diet will prevent exudative diathesis of chicks (*Gallus gallus*), liver necrosis in pigs (*Sus scrofa*) and rats (*Rattus* sp.), retained placentas in adult bovines, and white muscle disease in ruminants (National Research Council 1983). Although white muscle disease and retained placentas are the most typical symptoms of selenium deficiency in the bovine, other selenium-responsive diseases characterized by general unthriftiness, poor growth, and low tissue selenium also occur (National Research Council 1983). Probably the correction of these nonacute symptoms of selenium deficiency may be more economically critical than the more readily diagnosed diseases of white muscle disease and retained placentas.

High levels of dietary selenium are toxic to most animals. Acute selenium poisoning in the grazing animal is usually caused by the ingestion of large quantities of selenium accumulator plants in a brief period of time. This type of poisoning is infrequent since animals will usually avoid such plants (National Academy of Science 1980, National Research Council 1983). Clinical symptoms of selenium poisoning include liver cirrhosis, loss of long hair, soreness of feet, elongated hoof growth, stiffness and lameness due to erosion of the joints, atrophy of the heart, hemorrhaging, and emaciation (National Academy of Science 1980, McDowell 1983).

The biochemical role of selenium is complementary with that of vitamin E. Vitamin E has been implicated as a lipid antioxidant, scavenging free radicals and possibly singlet oxygen before they attack cellular and intracellular membranes. Inorganic selenium, as selenite, is an effective catalyst in vitro in the oxidation of thiol groups. Selenium, as a component of glutathione peroxidase (GSH-Px), protects membrane lipids against peroxidation either by removing the oxidant or by acting as a preventive antioxidant and removing radical-producing hydroperoxides. About 75–80% of the selenium in bovine erythrocytes is associated with glutathione peroxidase. Lipid peroxidation is therefore minimized by vitamin E and dietary selenium (Fraser 1985, National Research Council 1983).

Leinfelder et al. (1987) found that selenocysteine, the selenium analog of the sulfur-containing amino acid cysteine, is inserted into growing peptide chains as are the standard 20 amino acids. Selenocysteine may, therefore, be considered the 21st amino acid.

Similarities in the chemistry of selenium and sulfur led to investigations of possible biological interactions (Hill 1975). Biological interactions between selenium and arsenic, mercury, cadmium, and copper render selenium much less toxic than it is when present alone. Selenium has also been shown to reduce the toxicity of mercury and cadmium.

Selenium levels in blood and other tissues are indicative of a dietary intake of selenium up to the nutritional requirement of 0.1 ppm. As dietary selenium levels further increase in poultry, blood levels plateau and are no longer a reliable indicator of selenium levels (Scott 1973). Above the range of dietary adequacy of 0.1–0.3 ppm selenium for most species, the plasma or serum levels may plateau and then continue to rise slowly. Plasma or serum selenium concentrations rise rapidly with an excess of 0.3–0.5 ppm dietary inorganic selenium (Ullrey 1987). Possibly the same reaction takes place in ruminants. Measurement of the activity of GSH-Px is also used as an indicator of selenium levels in animals. The critical plasma selenium level used in the diagnosis of selenium deficiency in animals is 0.03 ug/ml (ppm) (McDowell et al. 1983). Williams (1980), using nonparametric classification of selenium data from cattle in northern California, specified 0.04 ppm whole blood selenium as the critical level in the diagnosis of selenium deficiency. Herds that were low in GSH-Px enzyme activity and had a whole blood selenium level below 0.04 ppm were compared with herds high in GSH-Px activity and with whole blood selenium levels above 0.04 ppm. Canadian workers (Puls 1981) feel that 0.09 ppm selenium in whole blood is critical (a level corresponding to 0.03 ppm selenium in serum or plasma). Maas and Koller (1985) indicate that levels of less than 0.3 ppm selenium (dry basis) in liver suggest selenium deficiency. These levels are less than those suggested by Puls (1981).

Dietary intake of 0.1 mg/kg (ppm) selenium will provide a satisfactory margin of safety against any dietary variables likely to be encountered by grazing cattle and sheep. Exact requirements may vary according to the form of selenium ingested and other dietary factors (McDowell et al. 1983). Selenium in plants ingested by animals is returned to the soil mainly in feces or urine, while some may be exhaled in the breath (Olson 1967).

In the United States, observations of selenium deficiency in ruminants have been somewhat limited to congenital and delayed white muscle disease in lambs and calves (Scott 1973).

In Carson Valley, Nevada, and adjoining areas inherently low in selenium, white muscle disease has been recognized (Vawter and Records 1947, Kuttler and Marble 1958). Alfalfa samples collected from Carson Valley were found to be below (< 0.05 ppm) the dietary requirement of 0.1 ppm selenium (Allaway and Hodgson 1964).

Poole et al. (1986) found that plasma selenium levels differed between northeastern (Elko County) and central (Lander/Eureka counties) Nevada. Animals grazing in Elko County had plasma selenium levels of 0.020 ppm, which were below the critical plasma selenium level (0.030 ppm) (McDowell et al. 1983), whereas animals grazing in central Nevada were found to be marginally adequate (0.029 ppm) in selenium. Animals in central Nevada were grazing crested wheatgrass (*Agropyron desertorum* or *A. cristatum*), which contained 0.13–0.17 ppm selenium (S. C. Poole and V. R. Bohman, unpublished data). Cattle raised in the Reno, Nevada, area on grass forage (pasture and haylage) containing 0.09 ppm selenium are deficient in selenium. Plasma selenium levels averaged 0.019 ppm selenium (S. C. Poole and V. R. Bohman, unpublished data).

Selenium can be supplemented by: (1) injection, (2) intraruminal pellets, or (3) salt or mineral mixtures (Nader et al. 1986). Results of supplementation are somewhat inconsistent (Hathaway et al. 1980, McDowell et al. 1983). Subcutaneous injections of selenium have been found to raise the blood selenium level but only for a period of about 90 days. Animals have responded favorably to injectable selenium supplementation in a study conducted in northern California (Mayland et al. 1985), an area similar to extreme northwestern Nevada in its selenium status. Cows receiving two intraruminal selenium boluses had blood selenium levels raised from deficient to adequate levels (< 0.02 to > 0.08 ppm selenium). Calves that were born to the supplemented cows had elevated blood selenium levels and gained faster from birth to weaning (Nelson and Miller 1987). Salt or mineral mixtures can be used to provide supplemental selenium to animals, although intake is variable. In Fallon, Nevada, whole blood selenium of cattle raised on native hay increased from 0.034 ppm selenium to 0.081 ppm selenium after the animals received a selenium-containing mineral mix for three months (T. Erquiaga, unpublished data).

Other cattle herds in Nevada have been evaluated for selenium. Cattle in White Pine County (eastern Nevada) that were raised on desert forage in the summer, followed by alfalfa in the fall, had average whole blood selenium levels of 0.51 ppm (0.41–0.62 ppm).

Blood selenium from cattle in western Nevada was much lower. Three cattle herds in the Fallon area had an average of 0.09 ppm blood selenium (0.05–0.14 ppm), while cattle from Yerington that grazed on forage from an alkali flat high in molybdenum had 0.048 ppm (0.03–0.08 ppm) selenium. None of the herds had a reported history of white muscle disease (H. Mayland, unpublished data).

SUMMARY

Selenium deficiency problems occur in western Nevada, extending from the Carson River valley northward toward Oregon. Forage is deficient in selenium in this area due to low selenium soils derived from recent volcanic deposits that are inherently low in selenium. Cattle raised in the Reno area are deficient in selenium. White muscle disease, a degenerative disease of the muscle in ruminants caused by insufficient selenium in the diet, has been reported in animals raised in the Carson River valley, south of Reno. Cattle low in tissue selenium have responded favorably to selenium supplementation in the Fallon area.

Variable amounts of selenium are found in forage in the north and central portions of the state, extending south to the western border of the Colorado River watershed. The areas of variable selenium include closed basins filled with alluvium and lacustrine sediments interspersed with mountain ranges of volcanic rocks, granites, and sediments. Cattle in northeastern Nevada had low tissue selenium, whereas animals grazing in the central part of the state were marginally adequate in this element. Differences between locations reflect the geological distribution of selenium. Forages grown on the high rangelands (above 2,300 m) of the selenium-variable area of the state are usually low in selenium. Forage produced at lower elevations is usually adequate. Forage sampled in southeastern Nevada contains adequate amounts of selenium for the grazing animal.

Selenium accumulator plants, which are usually considered toxic to animals, grow throughout Nevada on seleniferous geological formations. Although they can cause large losses of livestock, selenium indicator plants and subsequent livestock losses because of consumption of these plants are not recognized problems in Nevada.

Because selenium is variable in Nevada's rocks, soils, and forages, additional research should be conducted to locate and define areas of selenium adequacies and deficiencies for forage-fed animals. The status of animals that graze both selenium-deficient and selenium-adequate areas during the year needs evaluation. If selenium stores (i.e., liver stores) are adequate to meet the needs of animals during periods of inadequate intake, the problem is simplified. Tissue sampling (blood and liver) at critical intervals could be used to provide answers to this problem. Some areas of low selenium forage may be large enough that animals may spend their lives in these areas, with correspondingly lower growth and reproductive performance than desirable. If the seasonal status of selenium for animals is delineated, corrective measure could be initiated to minimize this problem when it exists.

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CLASSIFICATION OF THE RIPARIAN VEGETATION OF THE MONTANE AND SUBALPINE ZONES IN WESTERN COLORADO

William L. Baker[1]

ABSTRACT.—A classification of the riparian vegetation of part of western Colorado was developed by cluster analysis and ordination of 115 samples of relatively undisturbed vegetation. The classification of plant associations contains five montane riparian forests, three subalpine riparian forests, four lower subalpine willow carrs, three upper subalpine willow carrs, and one subalpine wetland.

Riparian ecosystems are widely recognized as important; yet in many areas their composition and structure have never been studied. Information on the composition and structure of riparian vegetation is essential if land managers are to be able to evaluate both the effects of their practices on riparian vegetation and their priorities for conservation. Particularly important for these purposes are data from relatively undisturbed examples of riparian systems. The purpose of this paper is to present the results of a plant association level classification of relatively undisturbed examples of the riparian vegetation of a part of western Colorado.

The study area (Fig. 1) is a 300 × 50-km part of the southern Rocky Mountains. The western boundary approximates the low-elevation limit of riparian vegetation dominated by *Populus angustifolia* and *Picea pungens*. The eastern study area boundary is the Continental Divide. The study focuses on larger streams from about 1,850 m in elevation to about 3,650 m (treeline).

Although *Populus angustifolia* extends along the Rocky Mountains from Mexico to southern Canada, *Picea pungens* occurs more spottily over a less extensive range (Little 1971). Thus, regions having montane forests similar to those in the study area may include only eastern Idaho and western Wyoming southward to northern New Mexico, parts of eastern Utah, and possibly northern Arizona. Similar regional limits may apply to the *Abies lasiocarpa–Picea engelmannii* riparian forests of the study area, as well as to many of the *Salix*-dominated wetlands (*carrs*).

Since European settlement, the riparian vegetation of the study area has been significantly altered. Most of the major streams have dams or water diversions. Gravel extractions and gold mining have altered many reaches. Upstream mining has introduced sediment into many stream channels. Livestock grazing of riparian vegetation is the most pervasive source of alteration and has resulted in widespread replacement of native plants by exotics.

METHODS

A goal of this study was to locate and sample sites (remnants) that are as free as possible of postsettlement land-use effects. To be considered suitable for sampling, a remnant had to: (1) have low coverage of exotic plants, such as *Poa pratensis* and *Taraxacum officinale;* (2) lack signs of recent livestock use, such as feces, trails, trampled areas, and grazed plants; (3) lack an altered species composition suggestive of past livestock use (cf. Skovlin 1984); (4) lack cut tree stems; (5) occur on a stream system without major channel alterations (e.g., channelization, dikes), major upstream dams, water diversions, or other water use, and without a high proportion of urbanized, overgrazed, recently logged, mined, or otherwise altered land area. A number of other local uses (e.g., gravel mining, homesites, highway effects) were also sufficient to exclude a site from sampling. Remnants were located by exhaustive field search. The length of most major streams in the study area was examined.

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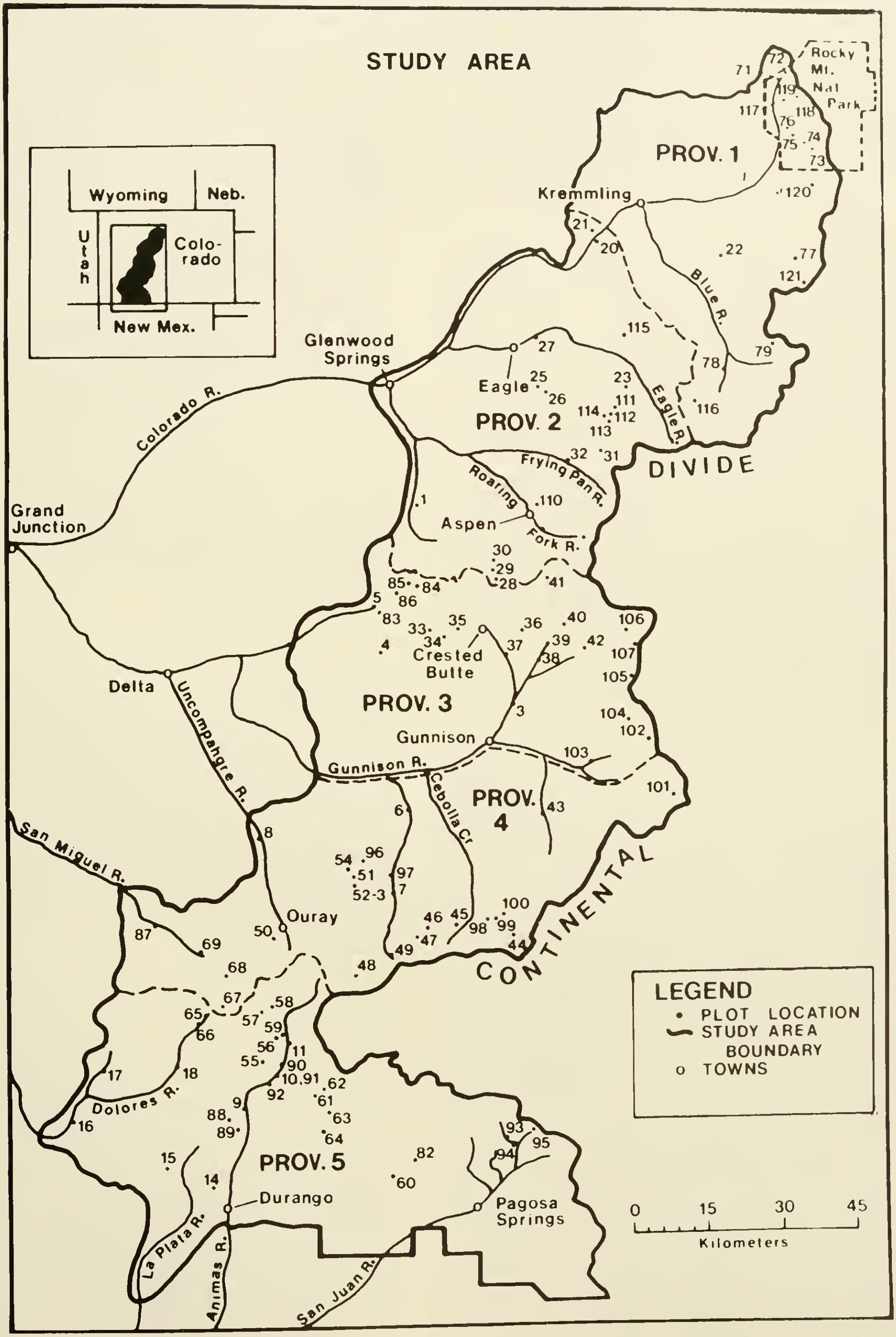
STUDY AREA
Wyoming
Neb.
Utah
Colo-rado
New Mex.
Rocky Mt. Nat Park
PROV. 1
PROV. 2
PROV. 3
PROV. 4
PROV. 5
Kremmling
Blue R.
Glenwood Springs
Eagle
Eagle R.
Colorado R.
Grand Junction
Frying Pan R.
Roaring Fork R.
Aspen
DIVIDE
Crested Butte
Delta
Uncompahgre R.
Gunnison
Gunnison R.
Cebolla Cr.
San Miguel R.
Ouray
CONTINENTAL
Dolores R.
La Plata R.
Animas R.
Durango
San Juan R.
Pagosa Springs
LEGEND
• PLOT LOCATION
STUDY AREA BOUNDARY
o TOWNS
0
15
30
45
Kilometers

Fig. 1. Study area map. Numbers next to dots on the map are stand numbers, also displayed on Figures 2 and 3.

A 20 × 50-m (0.1-ha) plot (e.g., Peet 1981) was used to sample the vegetation of a remnant. Within each plot I estimated percent canopy cover of all vascular plants: within 10% cover for species with greater than 50% cover, within 5% cover for species with 20–50% cover, within 2% for species with 8–20% cover, and within 1% for species with less than 8% cover.

Species nomenclature follows Kartesz and Kartesz (1980). Certain species could not be consistently distinguished in the field. *Amelanchier utahensis* and *A. alnifolia* are grouped under *A. utahensis. Rosa woodsii* may occasionally include other species of *Rosa. Salix drummondiana* and *S. geyeriana* may occasionally have been confused, as they are difficult to distinguish after flowering, when field sampling had to be conducted. *Carex microptera* may include some other species of *Carex* in section *Ovales. Poa leptocoma* and *Poa reflexa* grow intermixed and are difficult to distinguish when young. Voucher specimens are deposited at the Colorado State University Herbarium.

The analysis here is of mature stands (forests containing medium to large trees, carrs with full-grown willows) that are classified without inferring successional relationships from stand structure. It is thus a classification of contemporary remnants of presettlement vegetation, rather than a classification of "habitat types" (Pfister and Arno 1980) or "potential natural vegetation" (Driscoll et al. 1984). The presettlement vegetation in the study area has been altered, due to climatic changes, during the 125 years since settlement (Baker 1987). This classification of remnants thus describes the vegetation that would have been found along study area streams had European settlement not occurred. The approach follows closely that used earlier (Baker 1984).

I used Bray-Curtis ordination (Beals 1984) and the Ward method of cluster analysis (SPSS, Inc. 1986) to determine vegetation units. I first ordinated the entire data matrix of 115 stands and 462 species. More detailed interpretation of the ordination results and the relationships of the vegetation to environment is discussed elsewhere (Baker 1989).

I also clustered the complete data matrix. To reduce the amount of variation being considered, I took each of four clearly separable groups from the initial clustering dendrogram and reanalyzed their stands individually. These four groups I will refer to as montane forests, subalpine forests, lower subalpine carrs, and upper subalpine carrs. After these separate analyses most of the clearly separable groups on the clustering dendrograms were also separable on the ordination diagrams. Five stands, intermediate in composition, were reclassified. Discriminant analysis was used to assign eight outlier stands to one of the final vegetation units.

The level of classification detail is intended to be compatible with that in a previous plant association level classification (Baker 1984). Plant association names used here follow the general approach outlined in Baker (1984). Stand tables, which summarize mean cover and constancy of taxa in each association, were shortened by including only those taxa with greater than 70% constancy in at least one association of a group.

RESULTS AND DISCUSSION

Sixteen plant associations were distinguished, based on the ordination and cluster analysis results (Figs. 2, 3). The ordination and cluster analysis were congruent, in that associations identified by cluster analysis generally consisted of nonoverlapping stands on the ordination diagram (e.g., Figs. 2c, 2d). The composition, structure, and range of each association are described in the remainder of the paper.

1. Montane Forests

These forests (Table 1, Figs. 2a, 2b) have canopies dominated by either or both *Populus angustifolia* and *Picea pungens*, along with lesser amounts of a few other conifers. A well-developed shrub layer, with 20–50% total cover, is always present. The shrubby, small tree *Alnus incana* ssp. *tenuifolia* is nearly always present along the stream margin but varies in importance. Other shrubs common to all the associations include *Cornus sericea* and *Rosa woodsii.* The abundant forbs *Equisetum arvense* and *Smilacina stellata* occur in nearly all stands of all associations. The associations differ primarily in the composition of the tree canopy and shrub layer, as well as in environmental setting.

ASSOCIATION 1. *Populus angustifolia/Salix ligulifolia–Shepherdia argentea.* This association is tentatively described here based on only one stand (Table 1, Fig. 2b). It was an outlier on the first ordination and is not shown on the ordination of montane forests. Although field observations of degraded examples suggest that the association was formerly widespread, I could locate no other stands with low coverage of exotic plants and without current livestock grazing.

The association formerly dominated broad, open, low-elevation valleys on all major rivers throughout the study area, although the northernmost province lacks suitable low-elevation habitat. It has not been reported from other states, although it is likely that it extends into northeastern New Mexico, as I have observed it a few miles from the border on the San Juan River in province 1 (Fig. 1).

ASSOCIATION 2. *Populus angustifolia–(Picea pungens)/Alnus incana* ssp. *tenuifolia–Cornus sericea.* This association (Table 1, Figs. 2a, 2b), based on 13 stands, is characterized by a dense, sometimes impenetrable shrub layer dominated by *Cornus*, with abundant *Alnus* and often *Betula occidentalis* along the immediate stream bank. The understory is nearly always dominated by *Smilacina stellata*, with lesser amounts of *Equisetum arvense*.

The association occurs from eastern Idaho and western Wyoming (Youngblood et al. 1985a, 1985b) to southern Utah (Padgett and Youngblood 1986) and western Colorado. It has not been reported from New Mexico. In Colorado it has been reported from the White River Plateau (Hess and Wasser 1982) to the northwest of my provinces 4 and 5 (Fig. 1), and from several locations within the study area (DeVelice et al. 1984, Komárková 1986).

ASSOCIATION 3. *Picea pungens/Alnus incana* ssp. *tenuifolia.* This association (Table 1, Figs. 2a, 2b), based on eight stands, consists of a nearly pure canopy of *Picea pungens*, with a shrub layer somewhat similar to that of association 2, but with more *Alnus* and less *Cornus*. The understory, usually better developed than that in association 2, has about equal amounts of *Equisetum arvense* and *Smilacina stellata*.

There are no reports of the association from outside Colorado. Within Colorado it appears to be limited to my provinces 1, 2, and 3 (Fig. 1) but is most common in the San Juan Mountains in provinces 1 and 2. It was previously documented from the northern San Juan Mountains (DeVelice et al. 1984).

ASSOCIATION 4. *Picea pungens–Populus angustifolia/Alnus incana* ssp. *tenuifolia–Lonicera involucrata.* This association (Table 1, Figs. 2a, 2b), based on 10 stands, often has lesser amounts of *Pseudotsuga menziesii* associated with the two canopy codominants. The shrub layer has abundant *Lonicera*, often with lesser amounts of *Cornus sericea*, and always with *Alnus* along the stream bank. While *Equisetum arvense* and *Smilacina stellata* dominate the understory, as in associations 2 and 3, there are several forbs (e.g., *Actaea rubra* ssp. *arguta*, *Galium triflorum*, and *Geranium richardsonii*) much more common in this association.

The association has not been reported from outside Colorado. Within Colorado it has been previously reported in the study area in province 5 (Fig. 1), and I found it from the western part of province 1 through province 4. While it occurs in province 5, all locations I found were on rivers with upstream dams, making them unsuitable for sampling. I have not observed the association to the north of the study area in Colorado during previous fieldwork in that area. It is probably not in New Mexico, as association 5 occurs in similar habitats near the New Mexico border and has been reported in New Mexico (see below).

ASSOCIATION 5. *Abies concolor–Picea pungens–Populus angustifolia/Acer glabrum.* This association (Table 1, Figs. 2a, 2b), based on six stands, has the most diverse canopy of any of the montane forests, often with two or three other trees associated with the three canopy codominants. The shrub layer differs from that in the other montane forests in the abundance of *Acer* and in lesser amounts of *Cornus* and *Alnus*. The understory is quite different also, with abundant *Artemisia franserioides*, *Erigeron eximius*, *Pyrola asarifolia*, *Thalictrum fendleri*, and *Oryzopsis asperifolia*, along with the ubiquitous *Smilacina stellata*.

The association is probably restricted to southern Colorado and northern New Mexico. I found it only in that part of province 1 including and east of the Animas River (Fig. 1). It also occurs in the Sangre de Cristo Mountains in northern New Mexico (DeVelice et al. 1984).

TABLE 1. Mean percent cover (COV) and constancy (CON) of species in montane forest associations (ASSOC). Associations are: 1 = *Populus angustifolia/Salix ligulifolia–Shepherdia argentea*, 2 = *Populus angustifolia–(Picea pungens)/Alnus incana* ssp. *tenuifolia–Cornus sericea*, 3 = *Picea pungens/Alnus incana* ssp. *tenuifolia*, 4 = *Picea pungens–Populus angustifolia/Alnus incana* ssp. *tenuifolia–Lonicera involucrata*, 5 = *Abies concolor–Picea pungens–Populus angustifolia/Acer glabrum*.

	ASSOC 1		ASSOC 2		ASSOC 3		ASSOC 4		ASSOC 5	
Species	COV	CON	COV	CON	COV	CON	COV	CON	COV	CON
TREES										
Abies concolor (Gord. & Glend.) Lindl. ex Hildebr.	.0	.0	.0	.0	.0	12.5	.1	20.0	16.2	100.0
Juniperus scopulorum Sarg.	.0	.0	1.4	76.9	.2	50.0	.1	30.0	.0	16.7
Picea pungens Engelm.	.0	.0	7.8	69.2	28.1	100.0	22.5	90.0	26.7	100.0
Populus angustifolia James	25.0	100.0	16.9	100.0	.5	25.0	10.9	90.0	15.3	100.0
Populus tremuloides Michx.	.0	.0	2.3	15.4	.0	.0	2.2	30.0	2.4	66.7
Pseudotsuga menziesii (Mirbel) Franco var. *glauca* (Beissn.) Franco	.0	.0	2.4	46.2	1.6	75.0	6.4	80.0	5.0	66.7
SHRUBS										
Acer glabrum Torr.	.0	.0	.7	38.5	.8	37.5	2.4	70.0	8.0	100.0
Alnus incana (L.) Moench ssp. *tenuifolia* (Nutt.) Breitung	1.0	100.0	10.5	100.0	14.1	100.0	8.6	100.0	2.7	83.3
Amelanchier utahensis Koehne	.0	.0	2.9	61.5	3.3	50.0	3.4	100.0	1.9	100.0
Betula occidentalis Hook.	5.0	100.0	8.1	69.2	.0	.0	.0	10.0	1.7	16.7
Cornus sericea L.	1.0	100.0	24.8	100.0	6.1	87.5	7.1	70.0	1.4	50.0
Juniperus communis L.	.0	.0	.0	23.1	.0	25.0	.2	90.0	.3	33.3
Lonicera involucrata (Richars.) Banks ex Spreng.	.0	.0	2.5	30.8	4.9	75.0	16.6	90.0	3.5	100.0
Mahonia repens (Lindl.) G. Don	.0	.0	.0	30.8	.6	25.0	.1	50.0	.4	100.0
Prunus virginiana L.	.0	.0	3.5	30.8	1.5	37.5	.0	10.0	.2	66.7
Quercus gambelii Nutt.	.1	100.0	.1	15.4	1.4	50.0	.3	50.0	.0	16.7
Ribes inerme Rydb.	.0	.0	2.1	69.2	1.5	87.5	1.3	50.0	.5	50.0
Rosa woodsii Lindl.	.1	100.0	5.9	100.0	3.8	100.0	2.9	100.0	1.9	100.0
Rubus strigosus Michx.	.0	.0	.5	38.5	1.0	62.5	.9	30.0	.7	83.3
Salix drummondiana Barratt ex Hook.	.0	.0	.2	15.4	1.3	12.5	1.0	60.0	.4	33.3
Salix exigua Nutt.	10.0	100.0	1.0	69.2	.4	37.5	.0	20.0	.3	16.7
Salix ligulifolia (Ball) Ball ex Schneid.	25.0	100.0	.2	15.4	.3	12.5	.0	10.0	.0	.0
Shepherdia argentea (Pursh) Nutt.	15.0	100.0	.2	7.7	.0	.0	.0	.0	.0	.0
Symphoricarpos oreophilus Gray	.0	.0	.5	46.2	.9	62.5	2.3	90.0	.1	50.0
FORBS										
Achillea millefolium L. var. *lanulosa* (Nutt.) Piper	.1	100.0	.2	38.5	.1	100.0	.4	70.0	.2	66.7
Actaea rubra (Ait.) Willd. ssp. *arguta* (Nutt.) Hulten	.0	.0	1.7	61.5	.4	37.5	2.3	90.0	1.5	66.7
Artemisia franserioides Greene	.0	.0	.0	.0	.0	12.5	.1	10.0	5.7	66.7
Cirsium pallidum Woot. & Standl.	2.0	100.0	.0	23.1	.1	25.0	.1	70.0	.2	50.0
Clematis occidentalis (Hornem.) DC. var. *grosseserrata* (Rydb.) J. Prin.	.1	100.0	.5	38.5	.0	12.5	.0	30.0	.1	50.0
Epilobium angustifolium L.	.0	.0	.2	23.1	.7	75.0	.9	90.0	.2	66.7
Epilobium ciliatum Raf.	.1	100.0	.1	30.8	.0	12.5	.0	40.0	.0	.0

2. Subalpine Forests

These forests, with *Abies lasiocarpa* and *Picea engelmannii*, alternate with carrs in the same elevational range, above about 2,620 m. All of these subalpine forests have canopies codominated by *Abies lasiocarpa* and *Picea engelmannii* (Table 2). The shrub layer is generally sparser (15–30% total cover) than in the montane forests. There are no consistently present shrubs or forbs, probably due to the substantial elevational separation of the three associations.

ASSOCIATION 6. *Abies lasiocarpa–Picea engelmannii–Populus angustifolia/Lonicera involucrata*. This association (Table 2, Figs. 2c, 2d), based on seven stands, often has *Picea pungens* as a canopy associate and a shrub layer similar to that of association 7, but with less *Alnus* and *Salix drummondiana* and more *Amelanchier* and *Pachistima*. The forb layer

Table 1 continued.

	ASSOC 1		ASSOC 2		ASSOC 3		ASSOC 4		ASSOC 5	
Species	COV	CON	COV	CON	COV	CON	COV	CON	COV	CON
Equisetum arvense L.	4.0	100.0	4.1	76.9	11.0	100.0	3.1	100.0	1.6	83.3
Erigeron eximius Greene	.0	.0	.2	30.8	.6	25.0	.7	60.0	3.9	83.3
Fragaria vesca L. ssp. *americana* (Porter) Staudt	.0	.0	.0	15.4	.3	50.0	.7	80.0	1.0	66.7
Galium triflorum Michx.	.0	.0	.7	30.8	.5	50.0	3.1	80.0	1.2	83.3
Geranium richardsonii Fisch. & Trautv.	.0	.0	.5	46.2	.6	50.0	2.3	100.0	4.5	100.0
Heracleum lanatum Michx.	.0	.0	2.3	53.8	.3	50.0	2.6	70.0	.7	100.0
Heterotheca villosa (Pursh) Shinners	1.0	100.0	.0	7.7	.0	.0	.0	20.0	.0	.0
Mertensia ciliata (James ex Torr.) G. Don	.0	.0	.0	.0	.4	62.5	2.0	70.0	1.4	100.0
Mertensia franciscana Heller	.1	100.0	.0	.0	.0	12.5	.1	30.0	.0	.0
Mimulus guttatus Fisch. ex DC.	.0	.0	.2	15.4	.2	50.0	.0	30.0	.0	.0
Osmorhiza depauperata Phil.	.0	.0	.2	23.1	.2	50.0	2.7	70.0	2.4	83.3
Platanthera hyperborea (L.) Lindl.	1.0	100.0	.0	.0	.0	.0	.0	.0	.0	.0
Pseudocymopterus montanus (Gray) Coult. & Rose	.0	.0	.0	15.4	.1	50.0	.4	80.0	.6	83.3
Pyrola asarifolia Michx.	.0	.0	.3	38.5	.0	.0	1.4	20.0	2.0	83.3
Ranunculus pensylvanicus L. f.	1.0	100.0	.0	.0	.0	.0	.0	.0	.0	16.7
Smilacina racemosa (L.) Desf.	.0	.0	.2	15.4	.2	50.0	.6	80.0	.2	50.0
Smilacina stellata (L.) Desf.	4.0	100.0	8.2	92.3	10.6	100.0	6.8	100.0	11.5	100.0
Solidago canadensis L. var. *salebrosa* (Piper) M.E. Jones	.1	100.0	.1	46.2	.7	37.5	.0	40.0	.0	33.3
Thalictrum fendleri Engelm. ex Gray	.0	.0	.4	23.1	.9	50.0	1.1	80.0	10.7	100.0
Thermopsis divaricarpa A. Nels.	.1	100.0	.0	.0	.0	25.0	.3	10.0	.0	.0
Vicia americana Muhl. ex. Willd.	.0	.0	.1	76.9	.2	87.5	.1	60.0	.2	83.3
Viola canadensis L.	.0	.0	.2	30.8	.3	37.5	1.5	70.0	2.1	100.0
Graminoids										
Agrostis exarata Trin.	1.0	100.0	.1	38.5	.0	.0	.0	10.0	.0	.0
Bromus ciliatus L.	.0	.0	1.1	76.9	1.5	75.0	2.4	90.0	2.9	100.0
Calamagrostis canadensis (Michx.) Beauv.	.0	.0	.2	23.1	3.8	87.5	.3	40.0	1.7	50.0
Carex aquatilis Wahlenb.	5.0	100.0	.2	30.8	.8	37.5	.0	.0	.0	.0
Carex aurea Nutt.	.1	100.0	.0	.0	.0	12.5	.0	10.0	.2	16.7
Carex geyeri Boott	.0	.0	.2	23.1	8.1	37.5	3.0	60.0	1.2	33.3
Carex lanuginosa Michx.	4.0	100.0	.2	30.8	2.8	37.5	.0	10.0	.0	.0
Carex nebraskensis Dewey	2.0	100.0	.0	.0	.0	.0	.0	.0	.0	16.7
Carex rostrata Stokes ex With.	1.0	100.0	.1	7.7	.0	37.5	.0	.0	.0	.0
Carex scoparia Schkuhr ex Willd.	.0	.0	.5	30.8	.1	12.5	.6	30.0	2.4	66.7
Elymus glaucus Buckl.	.0	.0	.5	53.8	.9	50.0	2.4	70.0	1.8	83.3
Glyceria striata (Lam.) A.S. Hitchc.	1.0	100.0	.1	23.1	.0	.0	.0	10.0	1.7	16.7
Juncus balticus Willd.	10.0	100.0	.8	30.8	.8	50.0	.3	10.0	.0	.0
Juncus saximontanus A. Nels.	1.0	100.0	.2	7.7	.0	25.0	.0	20.0	.0	.0
Juncus tenuis Willd. var. *uniflorus* (Farw.) Farw.	1.0	100.0	.0	.0	.0	25.0	.0	.0	.0	.0
Oryzopsis asperifolia Michx.	.0	.0	.0	7.7	2.5	50.0	.1	20.0	2.2	100.0
Schizachne purpurascens (Torr.) Swallen	.0	.0	.0	.0	.6	25.0	.0	.0	1.0	66.7
Exotics										
Poa pratensis L.	5.0	100.0	.7	92.3	1.8	75.0	1.0	80.0	.4	83.3
Taraxacum officinale Weber	.1	100.0	.1	69.2	.1	62.5	.4	90.0	.2	66.7

has more *Actaea rubra* ssp. *arguta*, *Osmorhiza depauperata*, *Pyrola asarifolia*, *Smilacina stellata*, and *Elymus glaucus*.

There are no reports of similar vegetation from outside Colorado. Within Colorado I found the association only in provinces 1–4 (Fig. 1). DeVelice et al. (1984) have data from two stands in province 1. It is possible that the association extends into northern New Mexico, though there are no reports from that area.

Association 7. *Abies lasiocarpa–Picea engelmannii/Alnus incana* ssp. *tenuifolia–Lonicera involucrata–Salix drummondiana.* This association (Table 2, Figs. 2c, 2d), based on 11 stands, often has only the two codominants in the canopy. The shrub layer usually has *Alnus*, *Lonicera*, and *Salix* codominant, but *Alnus* may be absent at upper elevations of the association's elevational range, and *Salix drummondiana* may be absent from

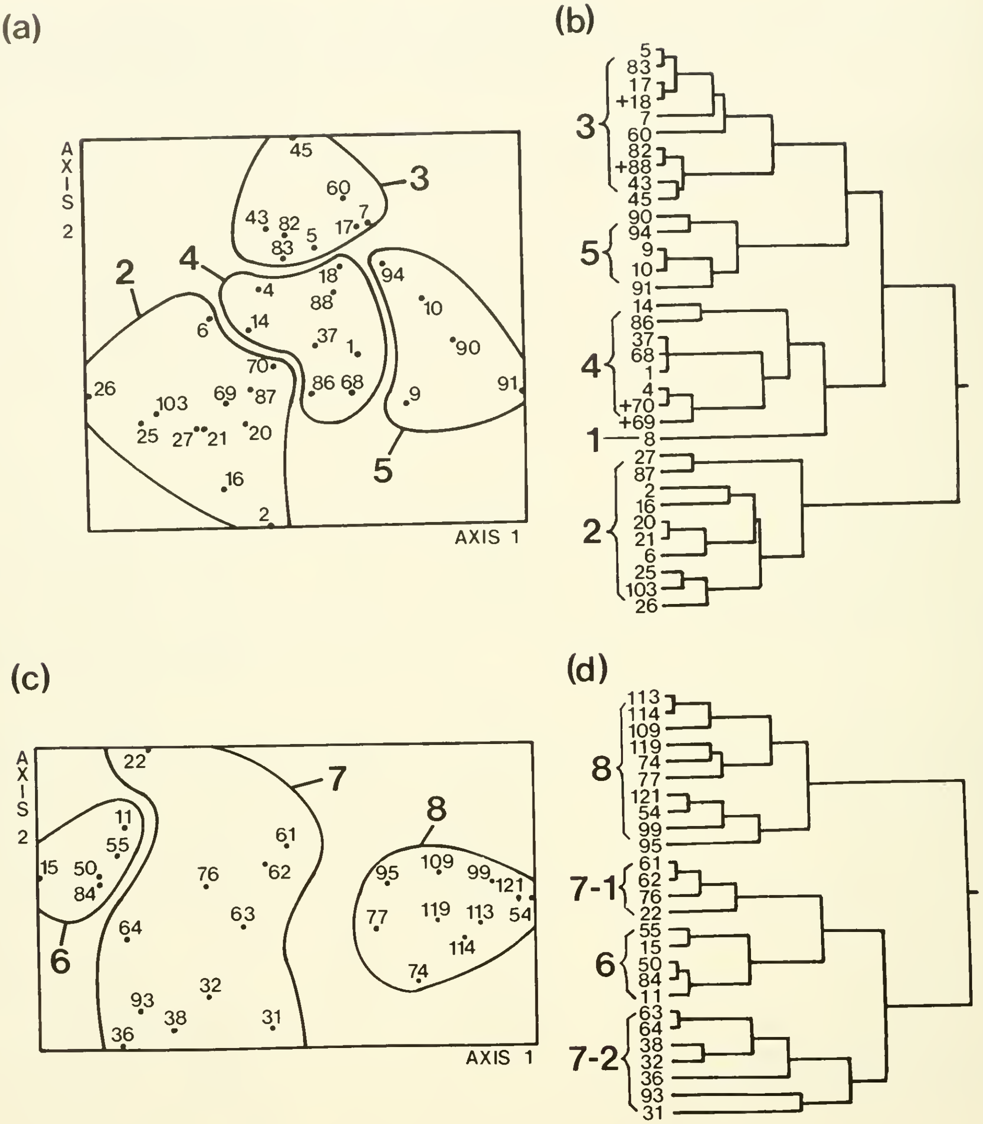

Fig. 2. Montane and subalpine forests. Numbers next to dots are stand numbers. (a) Montane forest ordination diagram. Associations are circled. Association numbers are: 1 = *Populus angustifolia/Salix ligulifolia–Shepherdia argentea*, 2 = *Populus angustifolia–(Picea pungens)/Alnus incana* ssp. *tenuifolia–Cornus sericea*, 3 = *Picea pungens/Alnus incana* ssp. *tenuifolia*, 4 = *Picea pungens–Populus angustifolia/Alnus incana* ssp. *tenuifolia–Lonicera involucrata*, and 5 = *Abies concolor–Picea pungens–Populus angustifolia/Acer glabrum*. (b) Montane forest cluster analysis dendrogram. Stand numbers are listed to the left of the lines of the dendrogram. Stand numbers preceded by a plus (+) indicate stands that were reclassified into another association. (c) Subalpine forest ordination diagram. Association numbers are: 6 = *Abies lasiocarpa–Picea engelmannii–Populus angustifolia/Lonicera involucrata*, 7 = *Abies lasiocarpa–Picea engelmannii/Alnus incana* ssp. *tenuifolia–Lonicera involucrata–Salix drummondiana*, 8 = *Abies lasiocarpa–Picea engelmannii/Cardamine cordifolia–Mertensia ciliata–Senecio triangularis*. (d) Subalpine forest cluster analysis dendrogram. Association 7 appears in two parts (7-1 and 7-2), which were merged.

some stands for unknown reasons. The forb layer, though similar to that of association 6, has more *Cardamine cordifolia*, *Mertensia ciliata*, *Oxypolis fendleri*, and *Calamagrostis canadensis*.

The association occurs from western Wyoming (Youngblood et al. 1985b) and northern Utah (Youngblood et al. 1985a) to western Colorado, where it is common in all provinces (Fig. 1) of the study area.

Association 8. *Abies lasiocarpa – Picea engelmannii/Cardamine cordifolia – Mertensia ciliata – Senecio triangularis*. This association (Table 2, Figs. 2c,2d), based on 10 stands, virtually never contains other tree species. The shrub layer is poorly developed but usually has 5–10% cover of *Ribes lacustre* and *Vaccinium myrtillus*. The association has the highest forb cover of any riparian association, but it consists mostly of the three named codominants and a few other species. The association nearly always consists of a very wet, narrow stream margin with dense, showy forbs and a drier, more rocky margin with more *Ribes* and *Vaccinium*, grading into adjacent drier forests.

The association is widely reported from Colorado (Baker 1984, Boyce 1977, Dix and Richards 1976, Peet 1981) and also occurs in northern New Mexico (DeVelice et al. 1984), but to the north of these areas it has not been reported, though related wet subalpine forests do occur in Wyoming, Montana, and Idaho. I found it in all the provinces (Fig. 1) of the study area.

3. Lower Subalpine Carrs

These carrs, dominated by tall willows (*Salix drummondiana*, *Salix geyeriana*, *Salix monticola*), occur between about 2,620 and 3,110 m in elevation. These willow carrs always consist of 3–5-m-tall, multistemmed *Salix* clumps scattered in a dense matrix of graminoids (*Carex* spp. and grasses), with lesser amounts of forbs. These four associations share some compositional characteristics (Table 3). All have abundant *Calamagrostis canadensis* (10–25% cover) and *Carex rostrata* (10–20% cover). All have 2–5% cover of *Cardamine cordifolia* and *Mertensia ciliata*. Most have lesser amounts of *Epilobium ciliatum*, *Epilobium angustifolium*, *Geranium richardsonii*, *Ligusticum porteri*, *Agrostis scabra*, and *Carex microptera*. The four associations are distinguished by the composition of the *Salix* canopy, by the amount of *Carex aquatilis* and a few forbs, and by differences in environmental setting.

Association 9. *Salix drummondiana–Salix monticola/Calamagrostis canadensis–Carex rostrata*. This association (Table 3, Figs. 3a, 3b), based on five stands, is distinguished from association 10 by the absence of shorter *Salix* spp. The carr often has very dense *Salix*, standing water, and scattered beaver ponds. Both association 9 and association 10 differ from 11 and 12 in having more abundant *Heracleum lanatum*, *Equisetum arvense*, and *Senecio triangularis*, and much less *Carex aquatilis*, all of which suggest a wetter habitat.

The association probably occurs from Idaho to Colorado, though data from Idaho (Tuhy and Jensen 1982, Mutz and Queiroz 1983) suggest *S. drummondiana* is more commonly associated with other species of *Salix* in that area. Nevertheless, carrs with *S. drummondiana*, *S. monticola*, and *Calamagrostis canadensis* do occur in Idaho (Tuhy and Jensen 1982), but they have not been reported from intervening areas in Wyoming or Utah. Within Colorado the association has been reported from the study area (Komárková 1986, plots 138, 167), where I found it scattered in provinces 1–4 (Fig. 1). I have also observed it, during previous fieldwork, to the north of the study area in the Yampa River drainage.

Association 10. *Salix drummondiana–Salix monticola–Salix planifolia–Salix wolfii/Calamagrostis canadensis–Carex rostrata*. This association (Table 3, Figs. 3a, 3b), based on four stands, is intermediate between the lower subalpine and upper subalpine carrs in that the *Salix* canopy consists of the 3–5-m-tall *S. drummondiana* and *S. monticola* mixed with the 1–3-m-tall *S. planifolia* and *S. wolfii*. The understory is similar to that of association 9, except that this association has somewhat more *Geranium richardsonii* and *Carex aquatilis*.

The association has not been reported from outside Colorado. Within Colorado I have found it only in the study area, scattered from provinces 1 to 4 (Fig. 1). It seems to be somewhat more common in the Eagle River drainage in province 4 than elsewhere.

Association 11. *Salix geyeriana–Salix monticola/Calamagrostis canadensis–Carex aquatilis–Carex rostrata*. This association

TABLE 2. Mean percent cover (COV) and constancy (CON) of species in subalpine forest associations (ASSOC). Associations are: 6 = *Abies lasiocarpa–Picea engelmannii–Populus angustifolia/Lonicera involucrata*, 7 = *Abies lasiocarpa–Picea engelmannii/Alnus incana* ssp. *tenuifolia–Lonicera involucrata–Salix drummondiana*, 8 = *Abies lasiocarpa–Picea engelmannii/Cardamine cordifolia–Mertensia ciliata–Senecio triangularis*.

	ASSOC 6		ASSOC 7		ASSOC 8	
Species	COV	CON	COV	CON	COV	CON
TREES						
Abies lasiocarpa (Hook.) Nutt.	6.7	85.7	14.5	100.0	11.2	90.0
Picea engelmannii Parry ex Engelm.	23.6	100.0	23.6	100.0	28.0	100.0
Picea pungens Engelm.	4.2	71.4	2.1	54.5	.0	10.0
Populus angustifolia James	10.9	100.0	.0	9.1	.0	.0
SHRUBS						
Acer glabrum Torr.	.7	71.4	1.3	18.2	.0	.0
Alnus incana (L.) Moench ssp. *tenuifolia* (Nutt.) Breitung	4.3	85.7	13.8	81.8	.2	10.0
Amelanchier utahensis Koehne	1.3	85.7	.3	54.5	.0	.0
Cornus sericea L.	4.4	71.4	1.7	27.3	.0	.0
Lonicera involucrata (Richars.) Banks ex Spreng.	12.3	100.0	14.5	100.0	.4	60.0
Pachistima myrsinites (Pursh) Raf.	2.6	85.7	1.0	36.4	.0	.0
Ribes inerme Rydb.	.9	57.1	.5	18.2	.0	.0
Ribes lacustre (Pers.) Poir.	.3	85.7	1.5	63.6	5.2	90.0
Ribes wolfii Rothrock	.5	57.1	1.8	72.7	1.3	50.0
Rosa woodsii Lindl.	3.0	71.4	.9	45.5	.1	10.0
Rubus strigosus Michx.	.6	85.7	.2	81.8	.0	20.0
Salix drummondiana Barratt ex Hook.	4.5	85.7	8.9	81.8	.5	20.0
Vaccinium myrtillus L.	.0	.0	2.0	63.6	7.3	90.0
FORBS						
Achillea millefolium L. var. *lanulosa* (Nutt.) Piper	.4	100.0	.1	63.6	.2	50.0
Actaea rubra (Ait.) Willd. ssp. *arguta* (Nutt.) Hulten	5.4	100.0	2.1	72.7	.0	.0
Angelica grayi Coult. & Rose	.0	14.3	.0	9.1	.5	80.0
Arnica cordifolia Hook.	.3	42.9	.8	54.5	3.9	100.0
Cardamine cordifolia Gray	.0	42.9	3.4	100.0	12.3	100.0
Epilobium anagallidifolium Lam.	.0	.0	.3	45.5	.4	70.0
Epilobium angustifolium L.	1.7	85.7	.8	100.0	.8	90.0
Epilobium ciliatum Raf.	.0	14.3	.0	45.5	.6	70.0
Equisetum arvense L.	2.3	57.1	2.4	63.6	.5	20.0
Erigeron eximius Greene	.9	71.4	.9	63.6	.0	.0
Erigeron peregrinus (Pursh) Greene	.6	42.9	.3	45.5	1.4	80.0

(Table 3, Figs. 3a, 3b), based on eight stands, differs from association 12 in the absence of shorter *Salix* spp. It is similar to association 9 in that both have very dense, tall *Salix*, standing water, and scattered beaver ponds. Both associations 11 and 12 have more *Potentilla fruticosa*, *Carex aquatilis*, and *Deschampsia cespitosa* than associations 9 and 10, again suggesting a somewhat wetter habitat for those associations.

The association has not been reported outside Colorado, though related *Salix geyeriana* carrs, lacking *Salix monticola*, are common in Idaho (Tuhy and Jensen 1982, Mutz and Queiroz 1983), western Wyoming (Youngblood et al. 1985b), and Utah (Youngblood et al. 1985a, Padgett and Youngblood 1986). Within Colorado the association has been reported from the eastern slope of the Front Range (Hallock et al. 1986, Hess 1981) and from north of the study area (Phillips 1977). I found it to be scattered throughout the length of the study area in all provinces. It is probably the most widely ranging willow carr association in Colorado.

ASSOCIATION 12. *Salix geyeriana – Salix monticola–Salix planifolia–Salix wolfii/Calamagrostis canadensis–Carex aquatilis–Carex rostrata*. This association (Table 3, Figs. 3a, 3b), based on seven stands, is similar to association 10 in that both are intermediate between lower subalpine and upper subalpine

Table 2 continued.

Species	ASSOC 6		ASSOC 7		ASSOC 8	
	COV	CON	COV	CON	COV	CON
Fragaria vesca L. ssp. *americana* (Porter) Staudt	.2	71.4	.4	45.5	.2	30.0
Galium triflorum Michx.	2.3	100.0	1.7	72.7	.1	10.0
Geranium richardsonii Fisch. & Trautv.	2.7	71.4	1.5	100.0	.8	30.0
Heracleum lanatum Michx.	2.2	85.7	4.0	81.8	.6	20.0
Ligusticum porteri Coult. & Rose	.2	42.9	.3	100.0	.4	70.0
Mertensia ciliata (James ex Torr.) G. Don	.9	57.1	2.2	90.9	11.8	100.0
Mertensia franciscana Heller	.6	42.9	1.5	45.5	.1	10.0
Mitella pentandra Hook.	.0	14.3	.5	54.5	.9	90.0
Orthilia secunda (L.) House	.5	42.9	1.0	81.8	.5	60.0
Osmorhiza depauperata Phil.	1.9	100.0	.9	90.9	.4	70.0
Oxypolis fendleri (Gray) Heller	.0	28.6	2.3	100.0	5.4	90.0
Polemonium delicatum Rydb.	.3	28.6	.6	9.1	1.9	80.0
Polygonum bistortoides Pursh	.0	.0	.0	9.1	.7	70.0
Polygonum viviparum L.	.0	.0	.3	27.3	.2	70.0
Primula parryi Gray	.0	.0	.0	9.1	.9	70.0
Pyrola asarifolia Michx.	2.2	71.4	.3	18.2	.3	10.0
Saxifraga odontoloma Piper	.0	.0	.7	54.5	2.6	100.0
Sedum rhodanthum Gray	.0	.0	.0	27.3	1.2	90.0
Senecio triangularis Hook.	.0	28.6	1.6	63.6	13.0	90.0
Smilacina racemosa (L.) Desf.	.5	85.7	.2	27.3	.0	.0
Smilacina stellata (L.) Desf.	6.7	85.7	2.6	54.5	.0	20.0
Streptopus amplexifolius (L.) DC.	.0	14.3	1.5	63.6	1.9	40.0
Thalictrum fendleri Engelm. ex Gray	3.4	85.7	1.3	90.9	.0	.0
Viola canadensis L.	.8	100.0	.2	36.4	.0	10.0
Graminoids						
Bromus ciliatus L.	1.6	71.4	1.0	81.8	1.5	80.0
Calamagrostis canadensis (Michx.) Beauv.	1.7	57.1	4.4	100.0	3.2	80.0
Carex aquatilis Wahlenb.	.0	14.3	.6	36.4	3.6	80.0
Cinna latifolia (Trev. ex Goepp.) Griseb.	.1	14.3	2.2	36.4	.0	.0
Deschampsia cespitosa (L.) Beauv.	.0	14.3	.6	36.4	2.6	80.0
Elymus glaucus Buckl.	1.5	85.7	.3	54.5	.2	10.0
Juncus drummondii E. Mey.	.0	.0	.0	9.1	.8	70.0
Luzula parviflora (Ehrh.) Desv.	.0	14.3	.6	72.7	2.1	100.0
Poa leptocoma Trin.	.0	.0	.0	.0	.8	80.0
Trisetum montanum Vasey	.0	.0	1.2	54.5	.0	10.0
Exotics						
Poa pratensis L.	.3	71.4	.1	54.5	.1	40.0
Taraxacum officinale Weber	.2	85.7	.1	90.9	.0	40.0

carrs because of the mixture of tall and short *Salix* species. The understory is similar to that of association 11, except that this association has more abundant *Epilobium ciliatum*, *Rorippa teres*, *Agrostis scabra*, *Geum macrophyllum*, and *Mertensia ciliata*.

The association has not been reported from outside Colorado. Within Colorado it has been found to the north of the study area (Phillips 1977) and within the study area in province 5 (Klish 1977). I found it in all provinces (Fig. 1) of the study area.

4. Upper Subalpine Carrs

These willow carrs always consist of 1–3-m-tall, multistemmed *Salix* clumps scattered in a dense matrix of forbs and graminoids. The three associations in this group share some compositional characteristics (Table 4, Figs. 3c, 3d). All three consistently have 25–60% cover of *Salix planifolia* but differ in codominant *Salix* species. All have substantial coverage of *Carex aquatilis* (14–21%), *Deschampsia cespitosa* (4–7%), and *Cardamine cordifolia* (3–7%), as well as lesser amounts of *Epilobium ciliatum*, *Ligusticum porteri*, *Mertensia ciliata*, *Oxypolis fendleri*, and *Pedicularis groenlandica*.

Association 13. *Salix planifolia–Salix wolfii/Caltha leptosepala–Carex aquatilis.* This association (Table 4, Figs. 3c, 3d), based on 10 stands, occasionally lacks *S. wolfii*,

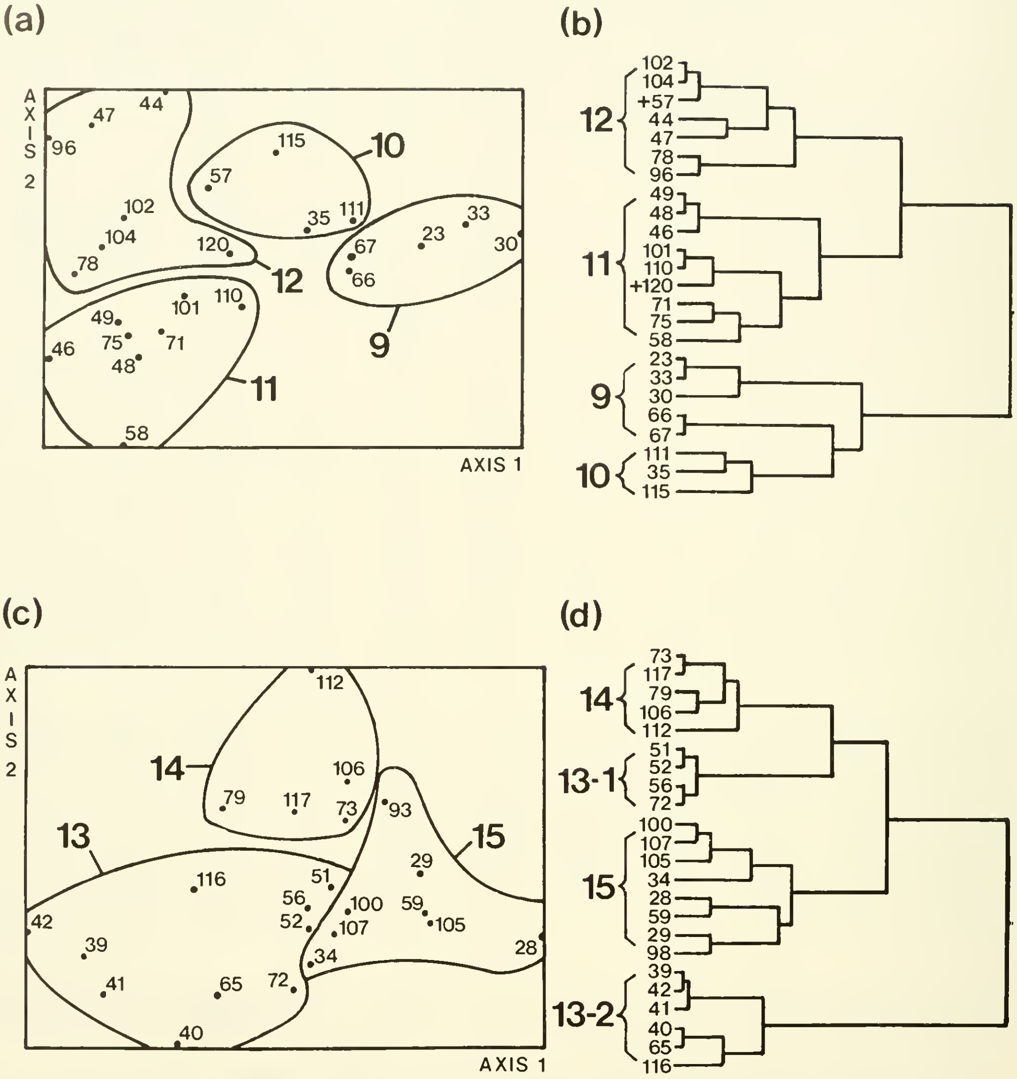

Fig. 3. Lower and upper subalpine carrs. (a) Lower subalpine carrs ordination diagram. Numbers next to dots are stand numbers. Associations are circled. Association numbers are 9 = *Salix drummondiana–Salix monticola/Calamagrostis canadensis–Carex rostrata*, 10 = *Salix drummondiana–Salix monticola–Salix planifolia–Salix wolfii/Calamagrostis canadensis–Carex rostrata*, 11 = *Salix geyeriana–Salix monticola/Calamagrostis canadensis–Carex aquatilis–Carex rostrata*, 12 = *Salix geyeriana–Salix monticola–Salix planifolia–Salix wolfii/Calamagrostis canadensis–Carex aquatilis–Carex rostrata*. (b) Lower subalpine carr cluster analysis dendrogram. Stand numbers are listed to the left of the lines on the dendrogram. Stand numbers preceded by a plus (+) indicate stands that were reclassified into another association. (c) Upper subalpine carrs ordination diagram. Association numbers are: 13 = *Salix planifolia–Salix wolfii/Caltha leptosepala–Carex aquatilis*, 14 = *Salix planifolia/Calamagrostis canadensis–Carex aquatilis*, 15 = *Salix brachycarpa–Salix planifolia/Caltha leptosepala–Carex aquatilis*, 16 = *Carex aquatilis–Carex rostrata–Deschampsia cespitosa* subalpine wetland. (b) Upper subalpine carr cluster analysis dendrogram. Association 13 appears in two parts (13-1 and 13-2), which were merged.

TABLE 3. Mean percent cover (COV) and constancy (CON) of species in lower subalpine carr associations (ASSOC). Associations are: 9 = *Salix drummondiana–Salix monticola/Calamagrostis canadensis–Carex rostrata*, 10 = *Salix drummondiana–Salix monticola–Salix planifolia–Salix wolfii/Calamagrostis canadensis–Carex rostrata*, 11 = *Salix geyeriana–Salix monticola/Calamagrostis canadensis–Carex aquatilis–Carex rostrata*, 12 = *Salix geyeriana–Salix monticola–Salix planifolia–Salix wolfii/Calamagrostis canadensis–Carex aquatilis–Carex rostrata*.

	ASSOC 9		ASSOC 10		ASSOC 11		ASSOC 12	
Species	COV	CON	COV	CON	COV	CON	COV	CON
SHRUBS								
Lonicera involucrata (Richars.) Banks ex Spreng.	1.2	100.0	.1	50.0	1.3	50.0	.6	42.9
Potentilla fruticosa L.	.2	20.0	.0	25.0	1.5	75.0	2.0	85.7
Salix drummondiana Barratt ex Hook.	41.0	100.0	18.0	100.0	1.4	37.5	.3	14.3
Salix geyeriana Anderss.	.0	20.0	.0	25.0	24.4	100.0	10.7	71.4
Salix monticola Bebb	17.0	100.0	15.0	75.0	24.4	87.5	17.6	85.7
Salix planifolia Pursh	.0	.0	10.5	100.0	.5	50.0	10.3	100.0
Salix wolfii Bebb ex Rothrock	.6	40.0	5.8	50.0	.2	50.0	16.0	100.0
FORBS								
Achillea millefolium L. var. lanulosa (Nutt.) Piper	.4	40.0	.3	75.0	.8	75.0	.4	100.0
Aconitum columbianum Nutt.	.6	80.0	.8	100.0	.1	12.5	1.2	71.4
Cardamine cordifolia Gray	3.8	100.0	4.3	100.0	3.4	75.0	3.0	85.7
Epilobium anagallidifolium Lam.	.1	60.0	.1	75.0	.3	37.5	.0	14.3
Epilobium angustifolium L.	.7	100.0	1.5	50.0	1.5	75.0	2.1	85.7
Epilobium ciliatum Raf.	.8	80.0	1.3	100.0	1.5	62.5	3.7	100.0
Equisetum arvense L.	3.4	80.0	3.1	100.0	1.9	62.5	.8	57.1
Erigeron peregrinus (Pursh) Greene	.4	40.0	.3	25.0	.2	62.5	1.0	85.7
Fragaria vesca L. ssp. *americana* (Porter) Staudt	.7	100.0	.1	50.0	1.3	75.0	.7	71.4
Galium trifidum L.	.0	40.0	.8	75.0	.4	37.5	.4	100.0
Geranium richardsonii Fisch. & Trautv.	.6	60.0	1.1	100.0	1.0	50.0	1.3	57.1
Geum macrophyllum Willd.	.8	80.0	3.5	100.0	1.8	100.0	3.3	100.0
Heracleum lanatum Michx.	5.2	100.0	5.8	100.0	1.3	37.5	1.0	42.9
Ligusticum porteri Coult. & Rose	1.2	60.0	1.3	100.0	2.1	100.0	2.5	100.0
Mertensia ciliata (James ex Torr.) G. Don	4.2	100.0	4.5	100.0	2.5	100.0	5.2	100.0
Mimulus guttatus Fisch. ex DC.	.2	60.0	.1	75.0	.3	37.5	.6	85.7
Oxypolis fendleri (Gray) Heller	1.5	100.0	.3	50.0	.3	37.5	.2	42.9
Pedicularis groenlandica Retz.	.0	40.0	.5	25.0	.0	12.5	1.3	57.1
Potentilla gracilis Dougl. ex Hook.	.0	40.0	.1	75.0	.3	37.5	.0	42.9
Rorippa teres (Michx.) R. Stuckey	.3	80.0	.3	100.0	.0	25.0	2.6	71.4
Saxifraga odontoloma Piper	.3	80.0	.0	25.0	.0	.0	.0	28.6
Senecio triangularis Hook.	1.0	80.0	2.3	100.0	.4	12.5	.5	42.9
Smilacina stellata (L.) Desf.	.4	40.0	.0	.0	.1	25.0	.6	71.4
Stellaria longipes Goldie	.2	40.0	.8	75.0	.3	75.0	.5	85.7
Thalictrum fendleri Engelm. ex Gray	1.0	60.0	.3	75.0	.2	50.0	.1	57.1
Veronica americana (Raf.) Schwein. ex Benth.	.0	20.0	.6	100.0	.8	37.5	1.0	85.7
Viola adunca Sm.	.0	40.0	.8	75.0	.0	12.5	.0	28.6
GRAMINOIDS								
Agrostis exarata Trin.	1.2	60.0	.5	50.0	.3	37.5	.2	28.6
Agrostis scabra Willd.	.5	80.0	.1	100.0	1.3	87.5	2.6	100.0
Alopecurus aequalis Sobol.	.2	40.0	.5	25.0	.6	50.0	1.7	71.4
Bromus ciliatus L.	.4	40.0	.3	75.0	.4	50.0	.9	42.9
Calamagrostis canadensis (Michx.) Beauv.	16.0	100.0	23.8	100.0	16.9	100.0	10.3	85.7
Carex aquatilis Wahlenb.	2.4	80.0	9.5	100.0	19.8	100.0	19.6	100.0
Carex microptera Mackenzie	1.5	80.0	1.3	100.0	1.9	100.0	2.2	100.0
Carex rostrata Stokes ex With.	13.0	80.0	19.5	100.0	11.5	100.0	13.7	100.0
Deschampsia cespitosa (L.) Beauv.	.6	40.0	1.0	50.0	4.5	75.0	4.3	85.7
Juncus saximontanus A. Nels.	1.6	60.0	.0	25.0	.8	50.0	1.0	57.1
Luzula parviflora (Ehrh.) Desv.	.1	60.0	.1	50.0	.4	12.5	1.3	57.1
Poa reflexa Vasey & Scribn.	.8	60.0	1.0	75.0	.0	25.0	.7	57.1
EXOTICS								
Poa pratensis L.	.4	60.0	1.3	75.0	.2	87.5	.9	85.7
Taraxacum officinale Weber	1.7	80.0	.3	100.0	.2	87.5	.1	100.0

TABLE 4. Mean percent cover (COV) and constancy (CON) of species in upper subalpine carr associations (ASSOC). Associations are: 13 = *Salix planifolia–Salix wolfii/Caltha leptosepala–Carex aquatilis*, 14 = *Salix planifolia/Calamagrostis canadensis–Carex aquatilis*, 15 = *Salix brachycarpa–Salix planifolia/Caltha leptosepala–Carex aquatilis*, 16 = *Carex aquatilis–Carex rostrata–Deschampsia cespitosa* subalpine wetland.

	ASSOC 13		ASSOC 14		ASSOC 15		ASSOC 16	
Species	COV	CON	COV	CON	COV	CON	COV	CON
SHRUBS								
Betula glandulosa Michx.	1.7	40.0	3.2	60.0	.9	12.5	.0	.0
Potentilla fruticosa L.	2.5	70.0	1.4	40.0	.4	37.5	.0	.0
Salix brachycarpa Nutt.	.0	10.0	.0	.0	11.9	87.5	.0	.0
Salix planifolia Pursh	20.5	90.0	33.0	100.0	53.8	100.0	.0	.0
Salix wolfii Bebb ex Rothrock	24.0	70.0	4.0	40.0	2.9	25.0	.0	.0
FORBS								
Achillea millefolium L. var. *lanulosa* (Nutt.) Piper	.9	90.0	.2	60.0	.5	75.0	.0	.0
Aconitum columbianum Nutt.	1.1	90.0	.3	80.0	2.9	100.0	.0	.0
Caltha leptosepala DC.	11.5	100.0	.1	60.0	12.9	87.5	10.1	100.0
Cardamine cordifolia Gray	4.0	100.0	2.8	80.0	6.6	100.0	2.5	100.0
Epilobium anagallidifolium Lam.	.7	100.0	.8	80.0	.9	62.5	.1	50.0
Epilobium ciliatum Raf.	1.1	100.0	1.4	100.0	.9	87.5	.1	100.0
Erigeron coulteri Porter	.7	70.0	.0	20.0	.4	37.5	.5	50.0
Erigeron peregrinus (Pursh) Greene	.3	40.0	.5	100.0	.8	62.5	.1	50.0
Fragaria vesca L. ssp. *americana* (Porter) Staudt	1.1	70.0	.5	80.0	.7	62.5	.0	.0
Galium trifidum L.	.0	10.0	.6	100.0	.0	12.5	.1	50.0
Geum macrophyllum Willd.	.6	80.0	3.4	80.0	2.0	50.0	.0	.0
Ligusticum porteri Coult. & Rose	2.0	100.0	1.2	80.0	2.5	87.5	.0	.0
Mertensia ciliata (James ex Torr.) G. Don	1.1	60.0	3.4	100.0	5.5	100.0	.5	50.0
Oxypolis fendleri (Gray) Heller	1.6	80.0	.1	100.0	1.6	87.5	.1	100.0
Pedicularis groenlandica Retz.	2.4	100.0	.8	80.0	2.5	75.0	2.6	100.0
Polygonum viviparum L.	.6	80.0	.2	60.0	.2	87.5	.0	.0
Potentilla gracilis Dougl. ex Hook.	.6	80.0	.0	20.0	.5	25.0	.0	.0
Saxifraga odontoloma Piper	.6	70.0	.0	40.0	.7	62.5	2.0	50.0
Sedum rhodanthum Gray	1.5	80.0	2.6	100.0	3.5	87.5	1.0	50.0
Senecio triangularis Hook.	2.2	40.0	3.0	80.0	6.6	100.0	4.0	50.0
Stellaria longipes Goldie	.5	90.0	.5	100.0	.6	87.5	.0	.0
Stellaria umbellata Turcz. ex Kar. & Kir.	.1	20.0	.2	40.0	.9	87.5	.1	50.0
Swertia perennis L.	.8	70.0	1.0	80.0	.5	37.5	.5	50.0
Veronica wormskjoldii Roemer & Schultes	.7	80.0	.8	100.0	1.3	100.0	1.6	100.0
Viola adunca Sm.	.2	20.0	1.0	100.0	.0	25.0	.1	50.0
GRAMINOIDS								
Agrostis scabra Willd.	.8	70.0	1.4	80.0	.2	37.5	.0	.0
Calamagrostis canadensis (Michx.) Beauv.	.8	80.0	25.0	100.0	2.1	62.5	2.5	50.0
Carex aquatilis Wahlenb.	21.0	100.0	17.4	100.0	14.1	75.0	32.5	100.0
Carex canescens L.	.0	.0	1.4	80.0	.4	25.0	.0	.0
Carex haydeniana Olney	.0	30.0	.0	20.0	.4	12.5	2.1	100.0
Carex microptera Mackenzie	.8	90.0	.2	60.0	.0	25.0	1.0	50.0
Carex norvegica Retz.	1.0	80.0	.8	80.0	1.4	62.5	.1	50.0
Carex rostrata Stokes ex With.	3.2	70.0	9.0	100.0	.5	37.5	7.5	50.0
Deschampsia cespitosa (L.) Beauv.	6.9	100.0	5.0	100.0	4.2	100.0	20.0	100.0
Festuca brachyphylla Schultes	.2	70.0	.2	60.0	.9	62.5	2.0	100.0
Luzula parviflora (Ehrh.) Desv.	.2	70.0	1.2	80.0	2.3	75.0	.0	.0
Phleum alpinum L.	.2	80.0	.5	80.0	.3	75.0	1.6	100.0
Poa leptocoma Trin.	.6	60.0	.8	100.0	2.1	87.5	.1	50.0
Poa reflexa Vasey & Scribn.	.7	80.0	.3	80.0	1.0	50.0	1.0	50.0
Trisetum wolfii Vasey	.4	60.0	.8	60.0	.5	75.0	.1	100.0
EXOTICS								
Poa pratensis L.	.8	40.0	.5	80.0	.0	37.5	.0	.0
Taraxacum officinale Weber	.8	80.0	.1	60.0	.3	50.0	.0	.0

though *S. wolfii* can also be nearly the sole dominant, particularly in the Taylor Park area in province 3 (Fig. 1). *Potentilla fruticosa* is a commonly associated shrub. The understory is similar to that of association 14, except for lesser coverage of *Carex rostrata*, *Mertensia ciliata*, *Senecio triangularis*, *Luzula parviflora*, and *Poa leptocoma*.

The association has not been reported from outside Colorado, though related pure *Salix wolfii* carrs, lacking *S. planifolia* and *Caltha leptosepala*, have been described in Utah (Youngblood et al. 1985a) and eastern Idaho and western Wyoming (Youngblood et al. 1985b). Within Colorado the association has been reported (1) from the White River Plateau (Hess and Wasser 1982), northwest of provinces 4 and 5 (Fig. 1), (2) to the north of the study area (Hess 1981), and (3) within the study area in provinces 3 (Komárková 1986) and 5 (Bierly 1972). I found the association to be common in all provinces (Fig. 1).

ASSOCIATION 14. *Salix planifolia/Calamagrostis canadensis–Carex aquatilis*. This association (Table 4, Figs. 3c, 3d), based on five stands, occasionally has substantial *Betula glandulosa* (7–8% cover) or *Salix wolfii* (5–15% cover), but often *S. planifolia* is the only shrub present. The understory is similar to that of association 13, except that the association has less of several forbs, discussed above, and more *Pedicularis groenlandica*, *Oxypolis fendleri*, and *Aconitum columbianum*. Association 13 rarely has more than 1% cover of *Calamagrostis canadensis*, which has 15–30% coverage in this association.

The association has not been reported from outside Colorado, with the exception of data from one site in Wyoming (Johnston 1984), which are not adequate to verify the occurrence of the association. It has been reported within Colorado from the eastern slope of the Front Range (Hallock et al. 1986) and within the study area in provinces 5 (Bierly 1972) and 3 (Komárková 1986). I found it in the study area only in provinces 3–5 (Fig. 1), which essentially comprise all of the study area north of the San Juan Mountains. Within this area it is much less common than association 13.

ASSOCIATION 15. *Salix brachycarpa–Salix planifolia/Caltha leptosepala–Carex aquatilis*. This association (Table 4, Figs. 3c, 3d), based on eight stands, often has a nearly pure, central, wetter area of dense, tall *S. planifolia*, with a more mixed, drier, rockier margin containing abundant *S. brachycarpa*. In this association *S. planifolia* may be 3 m or more tall. The understory is typically wetter than that in associations 13 and 14, which is reflected in the greater coverage of *Aconitum columbianum*, *Cardamine cordifolia*, *Mertensia ciliata*, and *Senecio triangularis*.

The association has not been reported from outside Colorado. Within Colorado it has been described from the White River Plateau (Hess and Wasser 1982, Johnston 1984) northwest of provinces 4 and 5. Within the study area I found it in provinces 1–4 (Fig. 1), but it probably also occurs in province 5.

5. Wetland

Only one wetland association is described. It occurs usually near the treeline or at the top of a small watershed, in settings that are similar to those of association 15, except that they have much flatter stream gradients and somewhat broader, deeper valleys.

ASSOCIATION 16. *Carex aquatilis – Carex rostrata – Deschampsia cespitosa* subalpine wetland. This association (Table 4), based on only two stands, is tentatively described here. Additional ungrazed stands suitable for sampling could not be located during the study. Substantial data on related wetlands are available in the literature; my data are reported to make them available for future research, rather than for a definitive treatment of the association.

Similar wetlands occur in Idaho (Tuhy and Jensen 1982, Mutz and Queiroz 1983, Youngblood et al. 1985b), western Wyoming (Youngblood et al. 1985a), Utah (Youngblood et al. 1985a, Padgett and Youngblood 1986), and western Colorado (Baker 1984, Johnston 1984, Komárková 1986), probably in all of the provinces (Fig. 1) of the study area, and most commonly on the northern slopes of the San Juan Mountains. In spite of its large range, this wetland is a minor vegetation type in the study area.

ACKNOWLEDGMENTS

Numerous individuals have contributed to this project. Lee Hackeling and Deb Paulson assisted with the fieldwork. B. Johnston, A. Winward, J. Tuhy, and K. Mutz provided unpublished materials. J. Scott Peterson, Sydney Macy, and D. Kuntz provided support in many forms. Financial support was provided by grants from the National Science Foundation (Grant SES-8601079), The Nature Conservancy, and The Colorado Natural Areas Program. I especially thank T. R. Vale for criticism, advice, and encouragement.

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WINTER HABITATS AND FOODS OF BLUE GROUSE IN THE SHEEPROCK MOUNTAINS, UTAH

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Gregory McDaniel[2], and Randy Berger[3]

ABSTRACT.—Winter habitat use and food habits of Blue Grouse (*Dendragapus obscurus*) were studied in an isolated Utah desert mountain range that contained little typical Douglas-fir (*Pseudotsuga menziesii*) winter habitat. Habitat use was concentrated in the Douglas-fir and pinyon (*Pinus edulis*)–juniper (*Juniperus spp.*) habitat. Douglas-fir and pinyon pine were the most consumed foods. Other foods that represented >15% of the composition of an individual fecal sample were limber pine (*Pinus flexilis*), mahogany (*Cercocarpus ledifolius*), juniper, and an *Antennaria–Cirsium* type. The breadth in winter diet indicates that Blue Grouse may successfully occupy other habitats when typical winter habitat is scarce.

Blue Grouse in the Intermountain West typically winter in snowbound, open stands of Douglas-fir at elevations above 1,830 m (Marshall 1946, Stauffer and Peterson 1985, Cade 1985). Mixed stands of subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), spruce (*Picea engelmannii*)/fir, and spruce/fir–lodgepole pine were used but generally received less use than Douglas-fir stands (Marshall 1946, Harju 1974, Cade 1985). The winter diet of Blue Grouse in the intermountain region is composed almost entirely of conifer needles and buds (Beer 1943, Stewart 1944, Marshall 1946). Douglas-fir dominates (up to 99%) the diet, although lodgepole and limber pine are regularly eaten in particular areas (Harju 1974, Cade 1985, Zwickel and Bendell 1986). Some atypical Blue Grouse winter foods recently identified include the genera *Juniperus*, *Cercocarpus*, *Abies*, *Picea*, and *Antennaria/Cirsium* (Zwickel and Bendell 1986). This disassociation from Douglas-fir apparently illustrates the ability of Blue Grouse to utilize a variety of habitats and forages during winter (Cade 1985, Zwickel and Bendell 1986).

Blue Grouse harvest trends from the Sheeprock Mountains, an isolated, desert mountain range located in central Utah in the Wasatch National Forest, are comparable to those from the Bear River Range in the Wasatch National Forest in the northeast section of Utah. However, the availability of typical Blue Grouse winter habitat is extremely different between the two areas. The Sheeprock Mountains contain only a few small, isolated stands of Douglas-fir; extensive Douglas-fir and subalpine fir habitat exists on the Bear River Range. The presence of a fall population of Blue Grouse on the Sheeprock Mountains during the fall migration period and the lack of Douglas-fir habitat indicated the Blue Grouse may winter in habitats other than Douglas-fir. The objectives of this study were to (1) determine habitats used by Blue Grouse during winter and (2) determine food habits of wintering Blue Grouse in the Sheeprock Mountains.

STUDY AREA

The Sheeprock Mountains are isolated by flat valleys and desert and contain moderately steep canyons. Elevation ranges from 1,830 m at the valley floor to peaks of 2,745 m. The five major habitats, excluding the valley floor, were sagebrush (*Artemisia* spp.) (40%), pinyon-juniper (30%), oak (*Quercus gambelii*)-mahogany-bitterbrush (*Purshia tridentata*) (28.5%), aspen (*Populus tremuloides*) (1%), and Douglas-fir (0.5%) (Richardson et al. 1982).

METHODS

Circular, nonoverlapping sample plots, 0.04 ha each, were randomly established in

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TABLE 1. Composition of plant fragments (%) in winter fecal droppings of Blue Grouse, Sheeprock Mountains, Utah.

		Collection tree			
Plant	Freq.[a]	Douglas-fir (4)[b]	Pinyon (4)	Mahogany (3)	Juniper (1)
Abies	5	<1[c] (0–1)[d]	0	1 (0–3)	5
Antennaria-Cirsium	2	0	14 (0–56)	0	0
Cercocarpus	2	0	0	10 (0–26)	0
Drapa	1	0	0	<1 (0–1)	0
Festuca	1	0	<1 (0–1)	0	0
Juniperus	6	0	3 (1–5)	<1 (0–1)	16
Phoradendron	1	<1 (0–1)	0	0	0
Picea	1	<1 (0–1)	0	0	0
Pinus	2	1 (0–3)	0	0	0
Pinus edulis	6	0	82 (37–97)	22 (0–67)	30
Pinus flexilis	2	0	0	<1 (0–2)	45
Pseudotsuga	8	98 (95–100)	<1 (0–1)	66 (0–100)	4
Unidentified seed	1	<1 (0–1)	0	0	0

[a] Number of composite samples (n = 12) in which plant was present.

[b] Number of composite samples.

[c] Percent composition based on 60 fields per composite sample.

[d] Range of % composition.

two canyons in the five major habitats. Plots were established in approximate proportion to the area occupied by each habitat to evenly distribute sampling intensity among the habitats. Douglas-fir was disproportionately sampled because of its known importance as winter habitat. Elevation of sample plots ranged from 1,830 to 2,600 m. Each plot was completely searched on snowshoes for evidence of grouse use. Grouse sightings, fecal droppings, tracks, snow roosts, and feeding sign (i.e., vegetative litter at the bases of trees) were noted. Any grouse sign observed outside the plots also was noted and assigned to a habitat. Plots were sampled during January–February 1986 and January 1987. Snow was present during all sampling periods.

We searched each habitat for winter fecal droppings during January 1987. Our goal was to collect 6–10 fecal droppings from under different trees in each habitat to obtain a random fecal sample. Droppings were collected randomly from under a tree in an attempt to obtain droppings from different birds if >1 roosted in a tree. Fecal droppings were collected under four Douglas-firs and four pinyon pines, but under only three mountain mahoganies and one juniper; none was found in sagebrush or aspen habitats. A composite sample was formed for each group of droppings collected under a tree. Droppings were frozen in air-tight plastic bags and sent to the Composition Analysis Laboratory (Range Science Department, Colorado State University, Fort Collins, Colorado) for content identification. Dried samples were homogenized by grinding over a 20-mesh (1-mm) screen. Twenty "fields" on each of three slides per composite sample were examined. Data were presented as percent relative density, an index of dry weight (Sparks and Malechek 1968). This procedure was identical to that employed by Zwickel and Bendell (1986). We assumed that potential biases associated with differential digestibility of various species (Gill et al. 1983) were minimal because of the woody nature of Blue Grouse winter diets (Zwickel and Bendell 1986).

RESULTS

We searched 131 plots, 30 each in pinyon-juniper and Douglas-fir, 33 in oak-mahogany-bitterbrush, 23 in sagebrush, and 15 in aspen. Grouse sign was found only in Douglas-fir plots (7 of 30). During searches for fecal droppings 3 grouse were flushed in Douglas-fir stands, and a group of 6–10 grouse were flushed from a pinyon-juniper stand. Tracks, feeding sign, and fecal droppings were found under pinyon pines in the vicinity where the 6–10 grouse were flushed.

Eleven plant genera were identified in the fecal samples (Table 1). Douglas-fir, pinyon pine, and juniper were found in ≥50% of the samples, but juniper never dominated an individual sample. Only Douglas-fir was found in samples collected under all species of trees.

Douglas-fir and pinyon pine were the most consumed foods and the dominant items in the diet under all collection trees, except the juniper (Table 1).

DISCUSSION

The abundance of sign found in Douglas-fir stands signified the importance of this relatively scarce habitat to Blue Grouse occupying the Sheeprock Mountains. Sign found in pinyon-juniper stands indicated that this habitat also was used by Blue Grouse. Because there was a much greater proportion of pinyon-juniper than Douglas-fir, our sampling efforts may have been inadequate to evaluate the relative importance of pinyon-juniper to Blue Grouse. However, wherever Blue Grouse occupied Douglas-fir and pinyon-juniper habitat simultaneously, Douglas-fir was more extensively used by Blue Grouse.

The diversity of species found in fecal droppings supported the conclusion of others that Blue Grouse exhibit adaptability in their winter diets (Bendell and Zwickel 1984, Cade 1985, Zwickel and Bendell 1986). Pinyon pine has not been previously identified as a winter food, although needles of other pines were commonly consumed in other areas (Marshall 1946, Harju 1974, Cade 1985, Zwickel and Bendell 1986). The presence of pinyon pine in droppings found under trees other than pinyon pine indicated that feeding on this species may be common in the Sheeprock Mountains. Although Zwickel and Bendell (1986) suggested that pines may be preferred to Douglas-fir as food, our data showed that Douglas-fir was more commonly consumed than pinyon pine.

This preliminary effort has documented Blue Grouse use of habitats other than Douglas-fir during winter on the Sheeprock Mountains. It appeared to us that Blue Grouse preferred the limited, available Douglas-fir stands. Although Blue Grouse both roosted and fed in pinyon pines, it is unknown whether pinyon-juniper stands, in the absence of Douglas-fir, could support the existing Blue Grouse population. Winter survival depends on meeting both nutritional and cover requirements, particularly during periods of severe weather. Pekins (1988) demonstrated that Douglas-firs provide protective microhabitats that decrease thermoregulatory costs during winter. Similar protection presumably is required for overwinter survival in other habitats.

Small Douglas-fir stands may be critical to the long-term dynamics of Blue Grouse in the Sheeprock Mountains and in other areas of the species range where typical winter habitat is isolated or not abundant. Small stands of Douglas-fir should be protected until it is demonstrated that alternate habitat types can support wintering Blue Grouse, particularly during rigorous winters.

ACKNOWLEDGMENTS

We thank Terry Shraeder for field assistance and the Bureau of Land Management for housing. This project, supported by the Utah Division of Wildlife Resources and the U.S. Forest Service, was conducted under the auspices of the Utah Cooperative Fish and Wildlife Research Unit, Utah State University.

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NEW SPECIES OF *HARASUPIA* WITH A REVISED KEY TO THE SPECIES (HOMOPTERA: CICADELLIDAE: COELIDIINAE)

M. W. Nielson[1]

ABSTRACT.—Five new species of *Harasupia* in the tribe Teruliini are described and illustrated. These include *austini*, *baja*, *mexicana*, *retrorsa*, and *ungula*, all from Mexico. A revised key to 12 known species is also given.

Harasupia Nielson is one of two genera in the tribe Teruliini that is Neogeic in distribution. The origin of the group, however, is believed to be Neotropical. All other genera in the tribe occupy the Neotropical realm except for one Ethiopian species of *Biadorus* Nielson. While most of the species of *Harasupia* occur in Mexico, its range extends as far south as Costa Rica (*bifurcata* Nielson) and north to Arizona (*snowi* [Lawson]). The latter species is common and has been collected on *Arctostaphylos* sp. in Arizona by the author. Host records of the remaining species are nonexistent or hosts are poorly known.

Descriptions of five new species in this paper add to seven previously known species and thus enhance the taxonomic affinities of the group (Nielson 1979, 1983). The genus is singularly characterized by a unique aedeagus with two appendagelike, asymmetrical structures of bizarre configurations in the distal 2/3 to 1/3 of the shaft. The gonoduct and gonopore are cryptic, or difficult to discern, which is unusual among leafhoppers.

Key to Males of *Harasupia*

1. Pygofer with small caudodorsal or caudoventral lobe 2

— Pygofer with long, prominent mesal spine on caudodorsal margin, spine directed ventrad (Fig. 1) .... *mexicana*, n. sp.

2(1). Aedeagus with 2 long, appendagelike processes originating subbasally (Nielson 1979, Fig. 111) . . . 3

— Aedeagus with 2 long or 2 short appendagelike processes originating medially or in distal 2/3 of shaft, respectively (Nielson 1979, Figs. 117, 143) 4

3(2). Aedeagus with 3 stout setae subdistally on ventral appendagelike process (Nielson 1983, Figs. 5, 6) .... *trispinata* Nielson

— Aedeagus with tuft of dense setae distally on ventral appendagelike process (Nielson 1979, Figs. 110, 111) .... *marginata* (Stål)

4(2). Style with short distal apophysis, length about as long as broadest basal part in lateral view (Nielson 1979, Figs. 122, 145) 5

— Style with very long distal apophysis, length much longer than broadest basal part in ventral view (Figs. 17, 22, 29) 7

5(4). Aedeagus with appendagelike processes separated near middle of shaft, appendages with spines or setae 6

— Aedeagus with appendagelike processes separated near distal 1/3 of shaft, appendages glabrous (Nielson 1979, Figs. 142, 143) .... *stipulata* Nielson

6(5). Aedeagus with ventral appendage with 4 long, fingerlike distal spines (Nielson 1979, Fig. 117) .... *sinistra* Nielson

— Aedeagus with ventral appendage with numerous distal setae (Nielson 1979, Fig. 126)....... .... *bifurcata* Nielson

7(4). Aedeagus with one or both appendagelike processes clawed, or with clawlike secondary structures (Fig. 14, Nielson 1979, Fig. 136) 8

— Aedeagus with appendagelike processes not clawed, ventral appendage with numerous spines (Nielson 1979, Fig. 132) .... *pustulata* (Spångberg)

8(7). Plate long and narrow (Figs. 18, 24); style glabrous (Figs. 17, 22) 9

— Plate long and very broad (Fig. 12); style with distal setae (Figs. 10, 11) .... *retrorsa*, n. sp.

9(8). Aedeagus with basal appendage clawed or with clawlike configuration in lateral view (Figs. 20, 27) 10

— Aedeagus with basal appendage not clawed in lateral view, but consisting of long process with cryptic gonoduct (Fig. 14) .... *austini*, n. sp.

10(9). Aedeagus with basal and distal appendages clawed or clawlike configuration in lateral view (Fig. 21) 11

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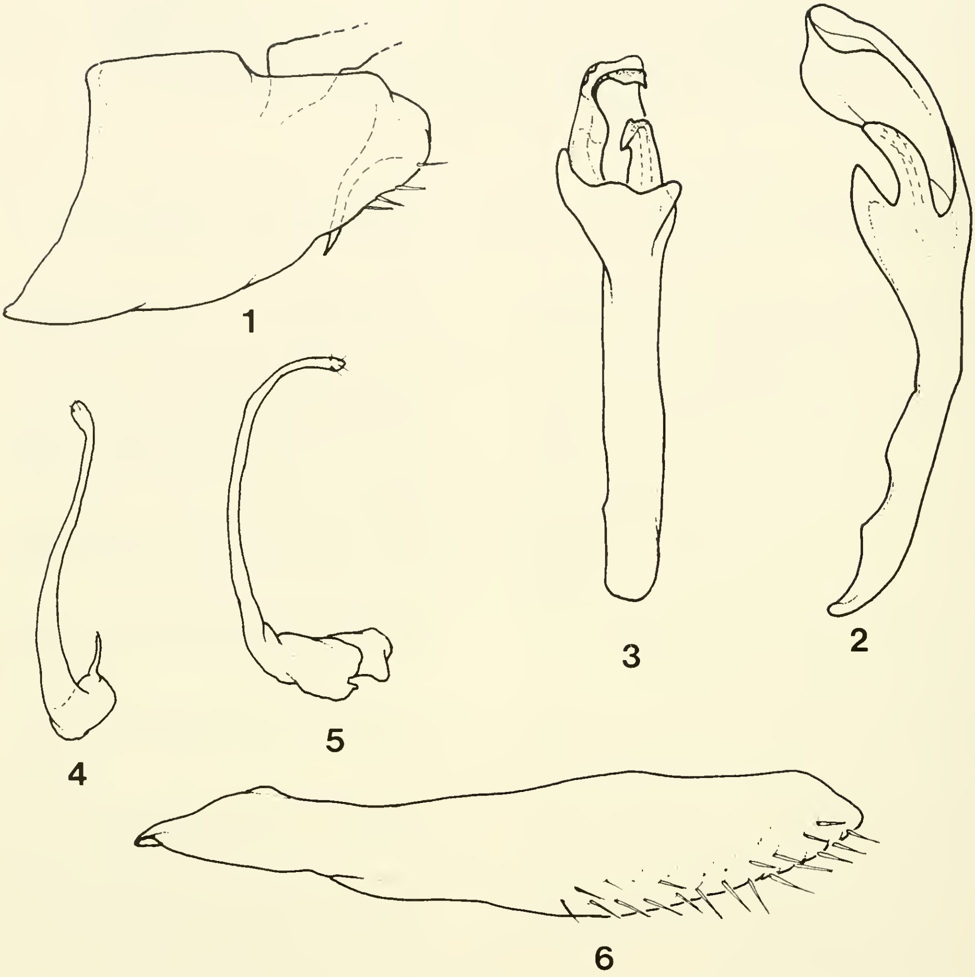


Figs. 1–6. *Harasupia mexicana*, n. sp.: 1, male pygofer, lateral view; 2, aedeagus, lateral view; 3, aedeagus, dorsal view; 4, style, ventral view; 5, style, lateral view; 6, plate, ventral view.

— Aedeagus with only basal appendage clawed, distal appendage long and narrow in lateral view (Fig. 20) .... *ungula*, n. sp.

11(10). Aedeagus with rami of basal and distal appendages long and narrow in lateral view (Nielson 1979, Fig. 136) .... *snowi* (Lawson)

— Aedeagus with basal rami of basal appendage bilobed, distal rami narrow, attenuated, and curved dorsally; rami of distal appendage broad and shallowly bilobed distally in lateral view (Fig. 27) .... *baja*, n. sp.

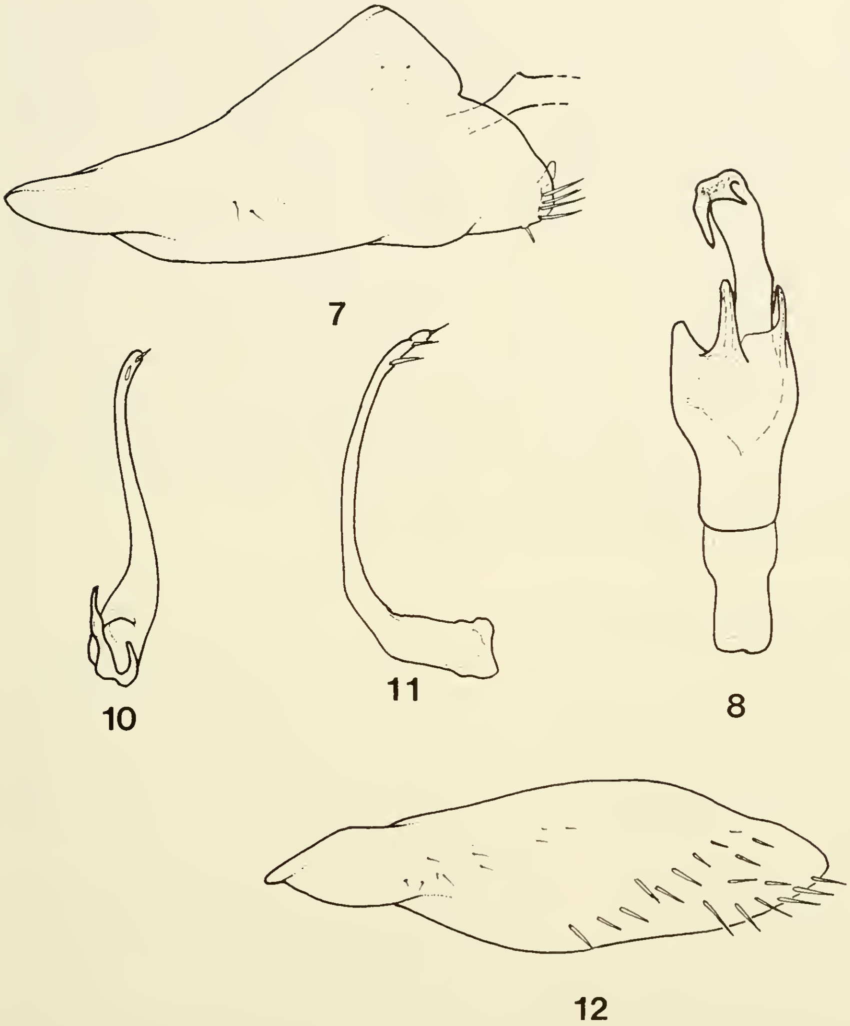
Harasupia mexicana, n. sp.

Figs. 1–6

LENGTH.— Male 7.20 mm.

General color dark brown with costa and claval cells translucent, some anteapical and apical cells partly translucent; crown creamy; eyes rufous; clypeus light creamy with rufous longitudinal band along lateral margins. Similar in general habitus to *ungula*, n. sp. but larger and with distinctive male genitalia.

Head narrower than pronotum; crown produced anteriorly, disc narrow, narrower than eyes; eyes large, elongate-ovoid; pronotum short, median length less than median length of crown; scutellum short, about equal in length to crown; forewing and venation typical (right forewing missing on type specimen); clypeus long and narrow, with faint but complete median longitudinal carina;



Figs. 7–12. *Harasupia retrorsa*, n. sp.: 7, male pygofer, lateral view; 8, aedeagus, dorsal view; 9, aedeagus, lateral view; 10, style, dorsal view; 11, style, lateral view; 12, plate, ventral view.

clypellus long, narrow, lateral margins expanded distally.

Male.—Pygofer in lateral view with long, narrow spine originating mesally on caudodorsal margin, spine directed ventrally (Fig. 1); aedeagus asymmetrical, basal appendage bilobed in dorsal view (Fig. 3) with lateral process containing gonoduct (Fig. 2), distal appendage broad in lateral view (Fig. 2); style with long, narrow apophysis, curved in lateral view and with distal setae (Figs. 4, 5); plate long and narrow, setaceous on ventral margin in distal half (Fig. 6).

Female.—Unknown.

Holotype (male).—Mexico: 24 mi W La Ciudad, 20.VII.1964, L. Kelton (CNC).

Remarks.—This species can be distinguished from all known members of *Harasupia* by the unique spine arising mesally on the caudodorsal margin of the pygofer.

Harasupia retrorsa, n. sp.

Figs. 7–12

Length.— Male 5.50 mm.

General color dark brown, veins of forewings deep brown, nearly all cells translucent; crown, pronotum, scutellum, and face light yellow; clypeus with rufous, broad, longitudinal band on lateral margins (specimen slightly teneral). Similar to *baja*, n. sp. in aedeagal characters.

Head narrower than pronotum; crown narrow, produced beyond anterior margin of eyes, disc narrower than width of eyes; pronotum and scutellum shorter than median length of crown; forewings typical; clypeus long and narrow, with faint but complete median longitudinal carina; clypellus narrow, lateral margins expanded distally.

MALE.—Pygofer in lateral view with small caudodorsal lobe (Fig. 7); aedeagus asymmetrical, basal appendage bilobed, with medial shaft containing gonoduct (Fig. 8), distal appendage asymmetrically bifurcate distally, with ventral distal rami projecting basad (Fig. 9); style with long, narrow apophysis, curved in lateral view with distal setae (Figs. 10, 11); plate long and very broad, with numerous setae (Fig. 12).

FEMALE.—Unknown.

HOLOTYPE (male).—MEXICO: Nayarit, 8 mi S Tepic, 18.X.1981, M. W. Nielson, in the author's collection (BYU).

REMARKS.—*Harasupia retrorsa* can be separated from *baja*, n. sp. by the broader plate, the narrower distal appendage, and the asymmetrical distal processes of the aedeagus from which the ventral rami project basad.

Harasupia austini, n. sp.

Figs. 13–18

LENGTH.—Male 5.80 mm.

General color blackish; forewings with costa and apex of clavus translucent; crown and face yellowish; pronotum and base of scutellum black; clypeus with pale, rufous, longitudinal band on lateral margins. Similar to *retrorsa*, n. sp. in aedeagal characters.

Head narrower than pronotum; crown produced beyond anterior margin of eyes, disc about as wide as width of eyes; eyes large, nearly globular; pronotum shorter than median length of crown and scutellum; scutellum with median length greater than median length of crown; forewings and venation typical; clypeus long and narrow, with faint but complete median longitudinal carina; clypellus narrow with lateral margins expanded distally.

MALE.—Pygofer in lateral view with small caudodorsal lobe (Fig. 13); aedeagus asymmetrical, with small spine near middle on dorsal margin in lateral view, and single, long, basal appendage containing gonoduct, distal appendage with two distal spines of unequal length projecting basad (Figs. 14, 15); style with long, narrow distal apophysis (Figs. 16, 17); plate long and very narrow, with microsetae distally (Fig. 18).

FEMALE.—Unknown.

HOLOTYPE (male).—MEXICO: Colima, Hwy 54, 14 mi NE Tecoman, 2,000 ft, 9.VIII.1982, C. W. & L. O'Brien & G. Wibner (BYU).

REMARKS.—From *baja*, n. sp., to which it is similar in certain male genital characters, *austini* can be separated by the small spine near the middle of the aedeagus, by the long, narrow basal appendage containing the gonoduct, and by the distal appendage with two dissimilarly shaped distal spines. This species is named for my grandson, Austin John Hammer.

Harasupia ungula, n. sp.

Figs. 19–24

LENGTH.—Male 7.20 mm.

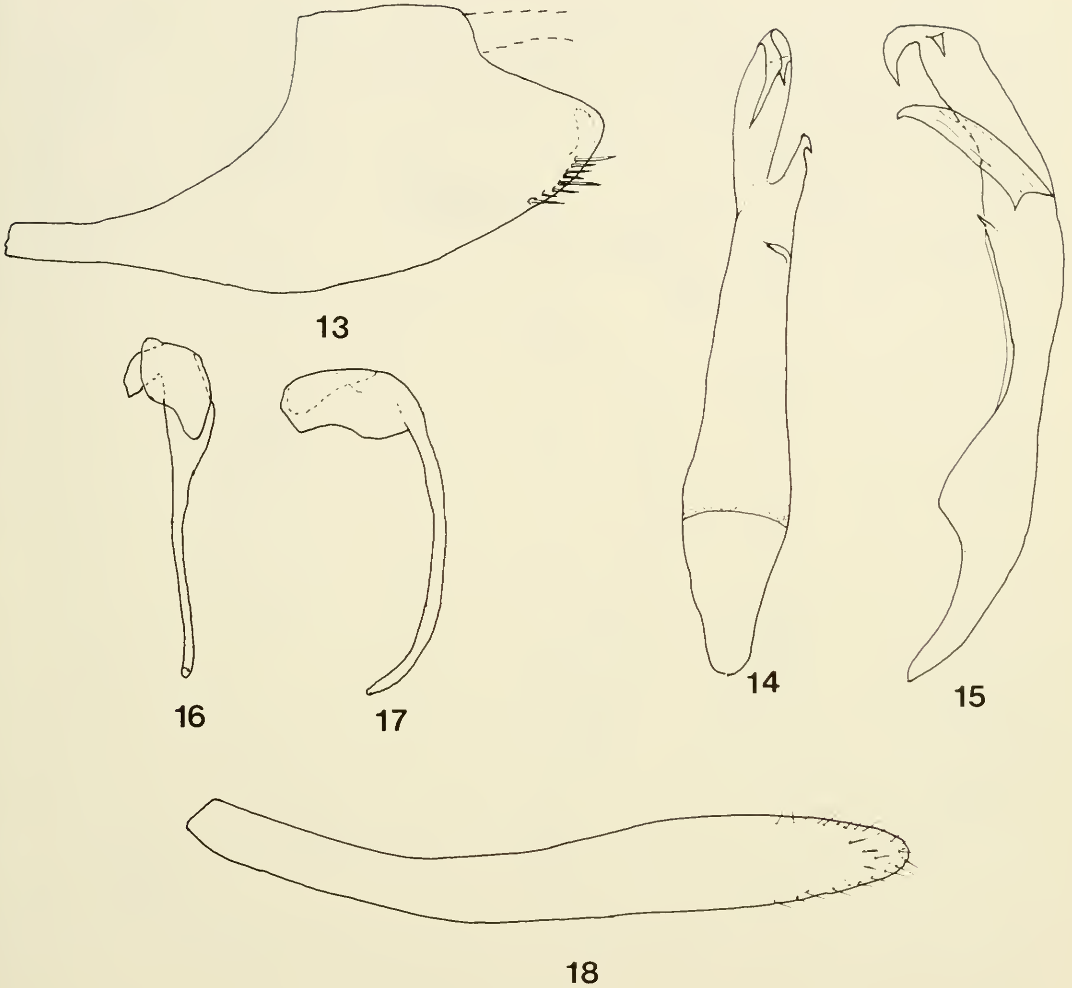
General color black; forewings blackish except for costa, cells of clavus, apex of anteapical cells, and base of apical cells, yellowish translucent, veins well marked; head and face yellowish except for lateral rufous band on margins of clypeus; pronotum and scutellum black. Similar to *austini*, n. sp. in male genital characters.

Head narrower than pronotum; crown produced beyond anterior margin of eyes, disc narrower than width of eyes; eyes large, semiglobular; pronotum short, median length less than median length of crown; scutellum with median length greater than median length of crown; forewings and venation typical; clypeus with weak but complete median longitudinal carina; clypellus narrow, lateral margins expanded distally.

MALE.—Pygofer in lateral view with small caudodorsal lobe (Fig. 19); aedeagus asymmetrical, basal appendage with dorsal rami enlarged, ventral rami narrow and containing gonoduct in lateral view (Fig. 20), distal appendage long and narrow in lateral view, compressed in dorsal view (Fig. 21); style with long, narrow distal apophysis, curved in lateral view (Figs. 22, 23); plate long, broad along middle third, setaceous (Fig. 24).

FEMALE.— Unknown.

HOLOTYPE (male).—MEXICO: 3 mi S El Salto, 21.VI.1964, L. Kelton (CNC).



Figs. 13–18. *Harasupia austini*, n. sp.: 13, male pygofer, lateral view; 14, aedeagus, dorsal view; 15, aedeagus, lateral view; 16, style, dorsal view; 17, style, lateral view; 18, plate, ventral view.

REMARKS.—This species can be distinguished from *austini*, n. sp. by its larger size, by the basal appendage of the aedeagus with enlarged basal rami and narrow distal rami containing the gonoduct, and by the distal appendage, which lacks a subdistal spine.

Harasupia baja, n. sp.

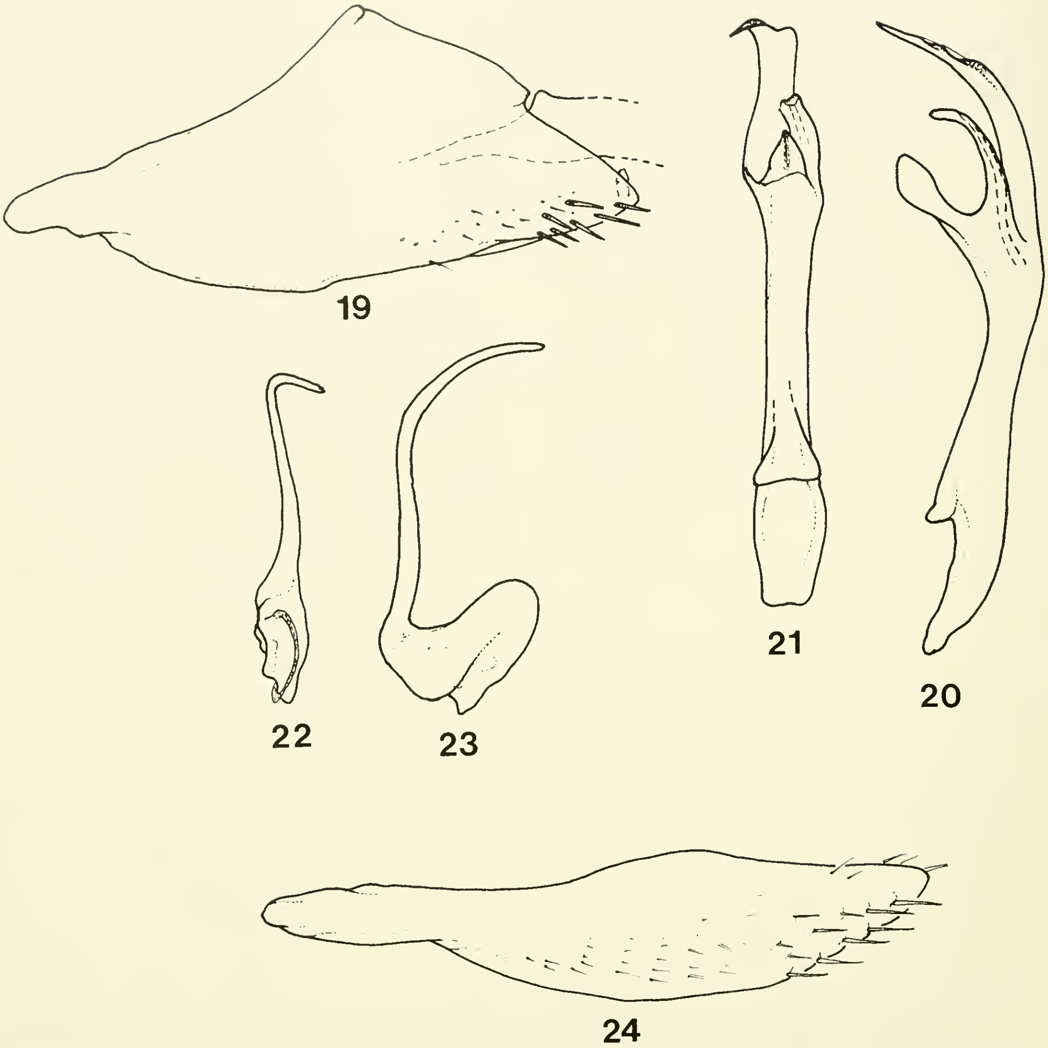
Figs. 25–30

LENGTH.—Male 6.20 mm, female 6.60 mm.

General color light to dark brown; crown yellowish; eyes dark brown; pronotum and scutellum tannish; forewings with veins blackish, cells mostly tannish translucent; face tannish. Similar to *mexicana*, n. sp. in some male genital characters.

Head narrower than pronotum; crown produced slightly beyond anterior margin of eyes, disc narrower than width of eyes in male, broader than eyes in female; pronotum shorter than median length of crown; scutellum with median length greater than median length of pronotum; forewings and venation typical; clypeus long and narrow, with faint but complete median longitudinal carina; clypellus narrow, lateral margins expanded distally.

MALE.—Pygofer in lateral view with small



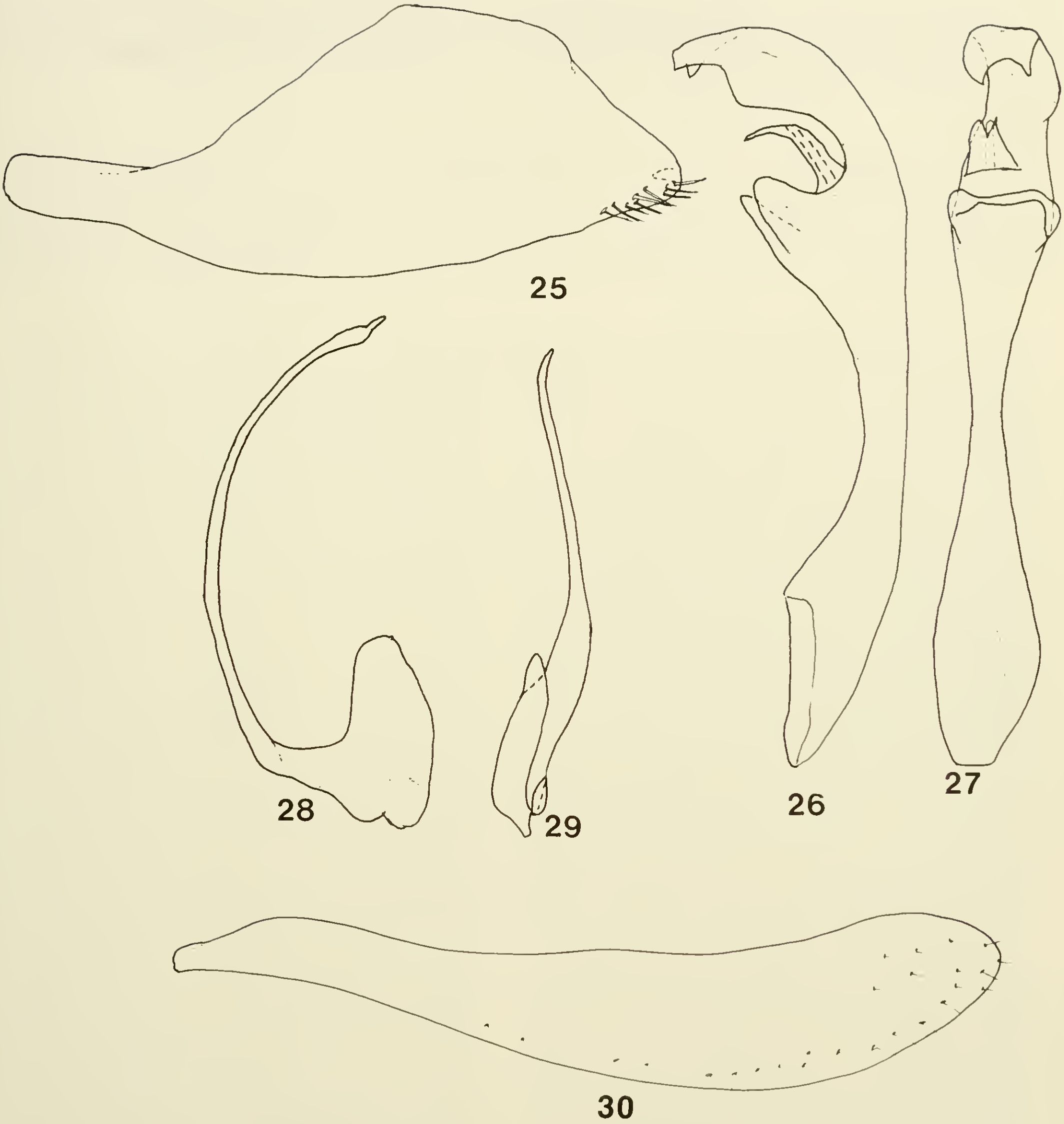
Figs. 19–24. *Harasupia ungula*, n. sp.: 19, male pygofer, lateral view; 20, aedeagus, lateral view; 21, aedeagus, dorsal view; 22, style, dorsal view; 23, style, lateral view; 24, plate, ventral view.

caudodorsal lobe (Fig. 25); aedeagus asymmetrical, basal appendage bilobed with narrow process medially and containing gonoduct in lateral view, distal appendage enlarged medially in lateral view, shallowly and broadly emarginate distally in dorsal view (Figs. 26, 27); style with distal apophysis very long and narrow, slightly swollen subdistally (Figs. 28, 29); plate long and narrow, with numerous microsetae distally and on ventral margin (Fig. 30).

FEMALE.—Sternum seven with posterolateral angles produced.

HOLOTYPE (male).—MEXICO: Baja California Sur, 4.3 km E La Burrera, 550 m, canyon-stream, 11–14.X.1978, Dozier & Westcott (BYU). Allotype (female), same data as holotype (BYU).

REMARKS.—*Harasupia baja* can be distinguished from *mexicana*, n. sp. by the small caudodorsal lobe on the male pygofer and by the lack of stylar setae. The holotype and allotype specimens are mounted on the same pin, with the male below the female.



Figs. 25–30. *Harasupia baja*, n. sp.: 25, male pygofer, lateral view; 26, aedeagus, lateral view; 27, aedeagus, dorsal view; 28, style, lateral view; 29, style, dorsal view; 30, plate, ventral view.

ACKNOWLEDGMENTS

Part of the material described here was borrowed from Agriculture Canada, Ottawa (CNC) through the kindness of Dr. K. G. A. Hamilton; the remainder was in the Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah (BYU), and in my personal collection. I thank Dr. H. Derrick Blocker, Kansas State University, Manhattan, for reviewing the paper and Mrs. Jeanette Price for illustrating all of the species except *austini* and *baja*, which were done by the author.

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QUADRAT AND SAMPLE SIZES FOR FREQUENCY SAMPLING MOUNTAIN MEADOW VEGETATION[1]

Jeffrey C. Mosley[2,3], Stephen C. Bunting[2], and M. Hironaka[2]

ABSTRACT.—Proper quadrat and sample sizes for sampling species frequency vary among vegetation types. This study found 10 × 10-cm quadrats most appropriate for frequency sampling dry mountain meadows when using a single quadrat size. If large, broad-leaved forbs are of special interest, 25 × 25-cm, 25 × 50-cm, or 50 × 50-cm quadrats may be useful. One hundred 10 × 10-cm quadrats adequately sampled most common species at alpha = 0.20 ± 10% frequency. In contrast, more than five hundred 0.29-m^2 circular plots usually were needed to sample individual species yield at alpha = 0.20 ± 20% of the mean.

Monitoring rangeland vegetation with quadrat frequency data recently has received interest from several authors (Hironaka 1985, West 1985, Mosley et al. 1986, 1987, Smith et al. 1986, 1987, Whysong and Brady 1987, Whysong and Miller 1987). Quadrat frequency sampling measures the presence or absence of a species in a given number of repeatedly placed small sample quadrats. Frequency is a desirable attribute for rangeland monitoring because it is stable, objectively measured, and simple to obtain (Brown 1954, Hyder et al. 1966). An important distinction separating frequency from other common vegetation attributes, such as yield, cover, and density, is that these other attributes are not influenced greatly by the plot size used to measure them. Frequency is affected by quadrat size, as well as plant size, plant distribution, and plant density (Kershaw and Looney 1985). Therefore, any interpretation of frequency estimates is of value only in relation to quadrat size. Some authors have criticized frequency sampling for its dependence on quadrat size (e.g., Weaver and Clements 1938), but this argument has no more credibility than saying that measurements from a ruler are valueless because they depend on the ruler (Curtis and McIntosh 1950).

Since frequency values depend on quadrat size, determining the proper-sized quadrat is important. Yet techniques for doing so are not entirely objective. A single quadrat size will sample some species more precisely than others because of their dissimilar plant sizes, distributions, and densities. However, several species within a plant community are usually of interest; thus, most sampling strategies strive to sample properly a maximum number of species while retaining precision for the most common species (Hyder et al. 1963). Curtis and McIntosh (1950) developed an accepted standard for determining proper quadrat size, concluding that an appropriately sized quadrat samples the most prevalent species at 63–86% frequency. Smith (1982) considered 20% a reasonable lower limit for measuring less abundant species. Plot sizes supplying extremely high or low frequencies are inappropriate since these values are too close to the extremes (0% and 100%) for setting reliable confidence limits. Consequently, as frequencies approach these extremes, their associated confidence interval decreases (Snedecor and Cochran 1980).

In addition to proper quadrat size, the proper number of quadrats (sampling intensity) is also important when sampling frequency. One approach for determining the proper number of quadrats employs species-area curves (Cain 1943, Oosting 1956). These species-area curves are derived by plotting the number of species sampled against an increasing number of small quadrats. The slope of the curve is initially steep but gradually flattens. The minimum number of quadrats needed can be found by locating that point where the curve begins to flatten. A problem with using species-area curves to determine frequency sampling intensity is that they do not reflect sample variation or the number of occurrences of a species. This is an important limitation for the statistical analysis of frequency data. A species is counted as sampled even if it is present only once; yet, as mentioned earlier, extremely low frequencies are statistically unacceptable. Species-area curves may be used to determine sample size for vegetation description, but they are inadequate when the aim is to monitor changes in species abundance. This latter goal requires a more rigorous method. Unfortunately, completely objective guidelines do not exist and sampling intensity decisions are resultantly always subjective. Nevertheless, they should be based on good judgment (Mueller-Dombois and Ellenberg 1974). Required sampling intensity for frequency sampling depends on two factors.

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First, frequency values obtained by a particular quadrat size will affect proper sampling intensity because frequencies are proportional data exhibiting a binomial distribution. Frequency data are skewed around low and high values but appear normally distributed about intermediate values. To compensate for the skewness, a larger sample size is needed for species or quadrat sizes supplying extremely high or low frequencies (Hyder et al. 1963). This binomial distribution of frequency values reemphasizes the need for proper quadrat sizes to provide intermediate frequencies.

Second, the number of quadrats needed also depends upon the level of precision desired. Because it is impractical to examine every individual within a plant community, vegetation must be sampled and inferences made about the population. Adequate sampling intensity is important if confidence is desired in sample estimates. And since each observation costs time and money, inevitably a compromise must be reached between precision and practicality, usually making it possible to evaluate only the more abundant species with reasonable accuracy (Mueller-Dombois and Ellenberg 1974). The dilemma of determining proper sampling intensity may be summarized best by Rice and Kelting (1955). They explain that in actual practice ecologists sample as many quadrats as their field experience indicates or their time and funds allow.

The purpose of this research was to provide guidelines for frequency sampling procedures in mountain meadows. Two related papers have explored potential uses of frequency data from mountain meadows of central Idaho (Mosley et al. 1986, 1987). This paper details the research that determined appropriate quadrat and sample sizes used in the two previously reported studies. For comparison, this study also examined an appropriate sample size for yield sampling mountain meadow vegetation.

METHODS

This study was conducted within dry mountain meadows of central Idaho located on the Boise, Payette, and Sawtooth National Forests. During the summers of 1982 and 1983 vegetation on study sites 1–12 was sampled for frequency and yield, while study sites 13–18 were sampled for frequency alone (Table 1). To sample variability within dry mountain meadows, we selected six sites from each of three range condition classes—good, fair, and poor. Condition was determined from U.S. Forest Service range analysis and trend study records. Botanical nomenclature followed Hitchcock and Cronquist (1973). Frequency sampling procedures followed those reported by Mosley et al. (1986), and yield sampling procedures followed Mosley et al. (1987). Rooted frequency of occurrence for individual species was recorded within 100 nested frequency quadrats per site, with 20 quadrats spaced along each of five transects. Frequency quadrats had several smaller quadrat sizes contained (nested) within one frame. Quadrat sizes were 5 × 5 cm, 10 × 10 cm, 25 × 25 cm, 25 × 50 cm, and 50 × 50 cm. Herbaceous yield was sampled by species within thirty 0.29-m^2 circular plots per site, allocated 10 plots along each of three transects.

Frequency data from all 18 study sites were analyzed to assess appropriateness of the different quadrat sizes for each study site. A proper-sized quadrat was the smallest quadrat that sampled a site's single most prevalent species at 63–86% (Curtis and McIntosh 1950). A lower limit of 20% was used to evaluate the ability of a quadrat size to measure less abundant species (Smith 1982).

TABLE 1. Study sites examined to estimate appropriate quadrat and sample sizes for frequency sampling mountain meadow vegetation.

Site no.	Site name	Elevation (m)	Ranger district	National forest
1	Ayers Meadow	1,950	Lowman	Boise
2	Bearskin Meadow	2,015	Lowman	Boise
3	Big Meadow	2,045	Lowman	Boise
4	Bruce Meadow	1,950	Lowman	Boise
5	Cache Creek	2,045	Lowman	Boise
6	Corduroy Meadow (a)	1,985	Lowman	Boise
7	Corduroy Meadow (b)	1,985	Lowman	Boise
8	Dead Cow Meadow	2,045	Lowman	Boise
9	Little East Fork	2,015	Lowman	Boise
10	Poker Meadow	1,985	Lowman	Boise
11	Pole Creek	1,985	Lowman	Boise
12	Stanfield Meadow	2,045	Lowman	Boise
13	Pen Basin	2,045	Cascade	Boise
14	Tyndall Meadow	2,135	Cascade	Boise
15	Hartley Meadow	2,135	McCall	Payette
16	Sater Meadow	1,920	McCall	Payette
17	Elk Meadow	2,045	Stanley	Sawtooth
18	Stanley Creek	1,985	Stanley	Sawtooth

Frequency data were also analyzed to assess sampling intensity on sites 1–12 (Table 1). Since proper sample size for frequency sampling is partially determined by quadrat size, proper sampling intensity was determined using the quadrat size deemed most appropriate in the first part of the study. To calculate an appropriate sample size for a particular species on a site, an estimate of the population variance, σ^2, was needed. This was supplied by the sample variance, s^2, and was calculated

$$s^2 = \frac{\Sigma p_i^2 - \frac{(\Sigma p_i)^2}{n}}{n(n-1)}$$

where p_1, p_2, . . . p_n were frequency percentages of a species by transect, and n was the number of transects sampled (Hyder et al. 1963). Estimated number of transects required, N, was calculated by

$$N = \frac{t^2ns^2}{(e.c.i.)^2}$$

where t was the tabular value, n was the number of transects already sampled, and *e.c.i.* was the expected-confidence-half interval (Hyder et al. 1963). Two different precision levels were evaluated, alpha = 0.10 ± 10% frequency and alpha = 0.20 ± 10% frequency. Since sample variances are correlated with frequency percentages, a complete set of e.c.i. values was needed to estimate the number of transects required for each species on each site. Values for e.c.i. standardized to within 10% of a mean frequency of 50% were taken from Hyder et al. (1963).

For comparison, yield data were analyzed to estimate adequate sampling intensity. Sample variance, s^2, was calculated

$$s^2 = \frac{\Sigma y_i^2 - \frac{(\Sigma y_i)^2}{n}}{n(n-1)}$$

where y_1, y_2, . . . y_n were dry weights (kg/ha) of species by transect, and n was the number of transects sampled. Estimated transects needed, N, was calculated

$$N = \frac{t^2ns^2}{b^2}$$

where t was the tabular value, n was the number of transects already sampled, and b was the bound on error. The precision level evaluated was alpha = 0.20 ± 20% of the mean.

RESULTS AND DISCUSSION

Quadrat Size

Hyder et al. (1963) determined a 23 × 23-cm quadrat was most appropriate for frequency sampling sagebrush-bunchgrass vegetation of eastern Oregon. On blue grama (*Bouteloua gracilis*) rangeland in Colorado, a 5 × 5-cm quadrat nested within a 41 × 41-cm quadrat was recommended (Hyder et al.

TABLE 2. Site comparison of smallest quadrat size that sampled the most prevalent species at 63–86% frequency.

Study site	Range condition class	Most prevalent species	Proper quadrat size (cm)
Cache Creek	Good	*Deschampsia cespitosa*	5 × 5
Elk Meadow	Good	*Carex* spp.	10 × 10
Hartley Meadow	Good	*Deschampsia cespitosa*	10 × 10
Poker Meadow	Good	*Deschampsia cespitosa*	25 × 25
Sater Meadow	Good	*Trifolium longipes*	10 × 10
Stanfield Meadow	Good	*Danthonia intermedia*	25 × 50
Bearskin Meadow	Fair	*Carex* spp.	25 × 25
Corduroy Meadow (a)	Fair	*Deschampsia cespitosa*	10 × 10
Dead Cow Meadow	Fair	*Trifolium longipes*	10 × 10
Pen Basin	Fair	*Danthonia intermedia*	50 × 50
Pole Creek	Fair	*Trifolium longipes*	10 × 10
Stanley Creek	Fair	*Deschampsia cespitosa*	25 × 25
Ayers Meadow	Poor	Annual forbs	50 × 50
Big Meadow	Poor	*Achillea millefolium*	10 × 10
Bruce Meadow	Poor	*Achillea millefolium*	10 × 10
Corduroy Meadow (b)	Poor	*Trifolium longipes*	10 × 10
Little East Fork	Poor	*Danthonia intermedia*	10 × 10
Tyndall Meadow	Poor	*Danthonia intermedia*	25 × 25

1965). In this study, proper quadrat size varied from 5 × 5 cm to 50 × 50 cm (Table 2). However, the 10 × 10-cm quadrat was the proper size if only one quadrat size was to be used on 10 of 18 sites, far more often than any other single quadrat size. Of the 10 sites where 10 × 10 cm was most appropriate, 3 sites were in good range condition, 3 in fair condition, and 4 in poor condition. Apparently, proper quadrat size does not vary with condition class.

Proper quadrat size did vary with apparent vegetation density. Visually the Ayers Meadow and Pen Basin sites had the lowest total plant cover with wider spaces between individual plants. These two sites were best sampled by the 50 × 50-cm quadrat. Conversely, vegetation at Cache Creek was the most dense and was best sampled by the smallest quadrat evaluated, 5 × 5 cm. Ayers Meadow and Pen Basin were the driest sites sampled, whereas Cache Creek was the moistest site studied.

It is noteworthy that the most prevalent species was always a graminoid or small forb. Large, broad-leaved forbs did not reach high frequencies until most graminoids and small forbs had exceeded the 86% limit. Table 3 compares the optimal quadrat size for several common species. For many of the larger or more widely spaced forbs, including *Aster* spp., *Agoseris glauca*, and *Antennaria corymbosa*, larger plot sizes such as 25 × 25 cm, 25 × 50 cm, and 50 × 50 cm appear more appropriate. Therefore, a nested quadrat containing 10 × 10-cm, 25 × 25-cm, 25 × 50-cm, and 50 × 50-cm quadrats appears most efficient for sampling a variety of mountain meadow species for frequency (Table 4). Note that usually less than 50% of all species encountered on a site were sampled within 20–86% frequency (Table 4).

Sample Size

Appropriate sampling intensity depends upon the objectives of a study. Extremely time-consuming, intensive vegetation sampling may be justified in research studies or in other studies in which a rare or highly variable species is of special concern. But most land management activities are more constrained by limited amounts of time and money and must often be satisfied with sampling at lower precision levels.

In this study as many as 196 transects of ten 0.29-m^2 circular plots each were needed to sample individual species yield, even at a conservative precision level (Table 5). This sample size is not practical considering the time and effort required to sample yield by species. Only one of the most common species, *Deschampsia cespitosa*, was adequately sampled with fewer than 100 quadrats. Since most land management personnel usually sample 30 or

TABLE 3. Quadrat size comparison of the number of sites where specific common species were sampled within a range of 20–86% frequency.

Species	No. of sites species encountered	Number of sites where species adequately sampled Quadrat size (cm)					Optimal quadrat size (cm)
		5 × 5	10 × 10	25 × 25	25 × 50	50 × 50	
GRAMINOIDS							
Carex spp.	18	11	13	11	11	10	10 × 10
Danthonia intermedia	17	6	11	10	10	7	10 × 10
Deschampsia cespitosa	13	7	9	7	5	5	10 × 10
Festuca idahoensis	8	1	3	5	4	4	25 × 25
Muhlenbergia filiformis	10	1	1	1	3	3	25 × 50
Stipa occidentalis	10	0	0	5	7	8	50 × 50
FORBS							
Achillea millefolium	13	6	9	8	6	6	10 × 10
Agoseris glauca	13	0	3	4	5	5	25 × 50
Antennaria corymbosa	17	0	2	6	7	8	50 × 50
Aster spp.	18	3	9	13	13	13	25 × 25
Cirsium vulgare	7	0	1	3	4	3	25 × 50
Gentiana calycosa	9	0	1	4	5	5	25 × 50
Senecio integerrimus	13	0	2	3	3	3	25 × 25
Trifolium longipes	14	7	7	4	4	4	5 × 5
Wyethia helianthoides	8	0	0	0	1	1	25 × 50

TABLE 4. Single quadrat size and nested quadrat group comparison of the number of species sampled within a range of 20–86% frequency.

Site no.	Total no. of species encountered	Number of species adequately sampled Quadrat size (cm)							
		5 × 5	10 × 10	25 × 25	25 × 50	50 × 50	10 × 10 25 × 25	10 × 10 25 × 25 25 × 50	10 × 10 25 × 25 25 × 50 50 × 50
1	27	2	4	6	7	8	6	7	8
2	20	3	6	9	7	7	10	10	10
3	19	4	6	7	6	7	9	9	10
4	27	4	5	7	12	13	9	15	16
5	20	2	1	1	3	5	2	4	6
6	22	2	8	9	8	8	10	10	11
7	24	4	9	9	9	7	11	12	12
8	19	3	6	10	10	8	11	12	12
9	27	4	7	7	7	8	10	10	11
10	23	3	4	5	7	8	8	11	12
11	30	3	6	12	13	13	13	16	16
12	18	1	7	8	9	9	8	9	10
13	21	2	4	9	10	12	9	10	12
14	21	2	4	7	7	8	8	9	10
15	9	1	1	1	3	4	2	4	5
16	18	2	5	4	5	5	6	8	8
17	13	3	3	5	4	4	5	5	5
18	23	1	8	12	13	11	12	14	14
Mean	21.2	2.6	5.2	7.1	7.8	8.0	8.3	9.7	10.4
S.E.	1.2	0.2	0.5	0.7	0.7	0.6	0.7	0.8	0.8

TABLE 5. Site comparison of the number of transects needed to sample yield of 15 common species at alpha = 0.20 ± 20% of the mean, as sampled with 0.29-m^2 circular plots allocated 10 per transect.

	Sites												
Species	1	2	3	4	5	6	7	8	9	10	11	12	Mean
GRAMINOIDS													
Carex spp.	24	8	43	37	3	122	7	30	9	13	2	9	26
Danthonia intermedia	263	3	52	35	*	267	16	3	5	68	23	21	69
Deschampsia cespitosa	*	*	*	*	2	3	*	4	12	2	13	4	6
Festuca idahoensis	261	8	14	8	*	*	39	*	269	*	*	*	100
Muhlenbergia filiformis	*	*	*	*	11	*	261	*	271	*	73	77	139
Stipa occidentalis	8	75	33	60	*	*	*	*	*	*	*	*	44
FORBS													
Achillea millefolium	15	9	6	4	*	*	11	76	8	*	18	*	19
Agoseris glauca	*	117	267	209	*	*	10	*	2	89	*	*	116
Antennaria corymbosa	119	51	83	*	267	265	261	26	31	6	267	*	138
Aster spp.	9	117	206	14	148	3	62	3	3	18	31	42	55
Cirsium vulgare	*	*	248	135	*	*	*	15	267	*	265	*	186
Gentiana calycosa	*	*	*	*	*	12	*	*	42	11	111	68	49
Senecio integerrimus	267	135	*	31	20	49	39	*	*	2	7	22	64
Trifolium longipes	120	267	89	5	267	*	21	15	10	65	7	*	87
Wyethia helianthoides	267	267	*	169	*	*	*	*	*	267	10	*	196

* = species not encountered.

fewer quadrats per site, our results emphasize that individual species yield estimates collected by land management personnel usually have very wide confidence limits. Many transects are needed per site because of the great variability in species yield. Conversely, a site's total herbaceous yield required only 2.7 ± 0.9 transects of ten 0.29-m^2 circular plots each to sample at alpha = 0.20 ± 20% of the mean. Mueggler (1976) found that similar sample sizes were needed for total yield in most mountain grassland and sagebrush-grass habitat types of western Montana.

The number of transects required to sample species frequency with 10 × 10-cm quadrats was more reasonable than sample size needed for species yield, varying from 6 to 19 transects at the 90% confidence level (Table 6). However, 5 transects of 20 quadrats each are probably the maximum practical for land managers frequency sampling mountain meadow vegetation. Each transect requires up to 30 minutes for two individuals to complete; additional plots or transects would be time prohibitive. Table 7 lists the number of frequency transects needed to sample with less precision. Most common species were sampled adequately with 5 transects at the 80% confidence level. Thus, a compromise must be reached between precision and practicality. Five transects may not meet the preferred precision level, but this sampling intensity probably provides acceptable results.

It is important to note that only 11 of the 15 most prevalent species and probably very few of the less common species were adequately sampled at alpha = 0.20 ± 10% frequency. This emphasizes that variance-based statistical tests are poorly suited to analyzing species frequency. Perhaps other statistical tests such as chi-square are better suited to analyzing frequency data. Unfortunately, we know of no way to independently calculate an adequate sample size for chi-square analysis.

CONCLUSION

Dense meadow vegetation was sampled best by small quadrats; more widely spaced vegetation required larger quadrats. However, a 10 × 10-cm quadrat is recommended as most appropriate for frequency sampling dry mountain meadows when using a single quadrat size. If large, broad-leaved forbs are of special interest, larger quadrats, such as 25 × 25 cm, 25 × 50 cm, or 50 × 50 cm, may prove valuable. A 10 × 10-cm quadrat appears to be the smallest quadrat necessary, and a 50 × 50-cm quadrat appears to be the largest size needed. If several species with greatly varying plant sizes, distributions, and densities need to be measured, more than one quadrat size may be required (Smith et al. 1987).

TABLE 6. Site comparison of the number of transects needed to sample 15 common species within 10% of a mean frequency of 50% with 90% confidence, as sampled with 10 × 10-cm quadrats allocated 20 per transect.

	Number of transects required Sites												
Species	1	2	3	4	5	6	7	8	9	10	11	12	Mean
GRAMINOIDS													
Carex spp.	32	29	26	7	4	13	12	22	1	5	10	1	14
Danthonia intermedia	7	10	9	12	6	5	2	17	7	15	12	2	9
Deschampsia cespitosa	*	*	*	*	5	11	*	4	9	9	12	9	8
Festuca idahoensis	3	4	4	15	*	*	4	*	*	*	*	*	6
Muhlenbergia filiformis	*	*	*	*	28	6	*	*	3	*	3	3	9
Stipa occidentalis	6	14	11	9	*	*	*	6	*	*	*	*	10
FORBS													
Achillea millefolium	4	6	7	5	*	*	9	70	10	*	5	*	15
Agoseris glauca	*	*	6	7	*	*	11	*	4	*	*	*	7
Antennaria corymbosa	8	16	5	*	*	12	*	9	8	6	7	6	9
Aster spp.	13	51	34	7	13	7	2	6	11	11	5	12	15
Cirsium vulgare	*	*	36	6	*	*	*	3	6	*	6	*	12
Gentiana calycosa	*	*	*	*	6	8	*	*	13	3	6	8	8
Senecio integerrimus	6	6	*	6	19	3	2	*	*	6	7	*	7
Trifolium longipes	5	38	9	3	18	*	9	12	73	13	8	*	19
Wyethia helianthoides	*	5	*	6	*	8	*	*	*	6	6	*	7

* species not encountered

TABLE 7. Site comparison of the number of transects needed to sample 15 common species within 10% of a mean frequency of 50% with 80% confidence, as sampled with 10 × 10-cm quadrats allocated 20 per transect.

	Number of transects required Sites												
Species	1	2	3	4	5	6	7	8	9	10	11	12	Mean
GRAMINOIDS													
Carex spp.	17	15	14	4	3	7	7	12	1	3	5	1	8
Danthonia intermedia	3	5	5	7	3	3	1	9	4	8	6	1	5
Deschampsia cespitosa	*	*	*	*	3	6	*	2	5	5	6	5	5
Festuca idahoensis	2	2	2	8	*	*	2	*	*	*	*	*	4
Muhlenbergia filiformis	*	*	*	*	15	3	*	*	2	*	2	2	5
Stipa occidentalis	3	7	6	5	*	*	*	3	*	*	*	*	5
FORBS													
Achillea millefolium	2	3	4	3	*	*	5	8	5	*	3	*	5
Agoseris glauca	*	*	3	4	*	*	6	*	2	*	*	*	4
Antennaria corymbosa	5	8	3	*	*	6	*	5	5	3	4	3	5
Aster spp.	7	27	18	4	7	4	2	3	6	6	3	6	8
Cirsium vulgare	*	*	19	3	*	*	*	2	3	*	3	*	6
Gentiana calycosa	*	*	*	*	3	4	*	*	7	2	3	5	4
Senecio integerrimus	3	3	*	3	10	2	1	*	*	3	4	*	4
Trifolium longipes	3	20	5	2	10	*	5	6	38	7	4	*	10
Wyethia helianthoides	*	3	*	3	*	5	*	*	*	3	4	*	4

* species not encountered

Species frequency in mountain meadows was adequately sampled at a practical sampling intensity of one hundred 10 × 10-cm quadrats. In contrast, precise estimates of individual species yield required sample sizes beyond practical levels for land management personnel. Total herbaceous yield of mountain meadows was adequately sampled with a practical sample size of thirty 0.29-m^2 circular plots.

ACKNOWLEDGMENTS

Research was funded in part by USDA Science and Education Administration Grant No. 59-2161-1-2-082-0. We wish to thank personnel of the Boise, Payette, and Sawtooth National Forests for their assistance with this study.

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FOODS AND FEEDING PERIODICITY OF THE WHITE RIVER SPRINGFISH, *CRENICHTHYS BAILEYI*

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Abstract.—White River springfish collected in August and December 1966 from Hot Creek Spring, Nevada, fed primarily on amphipods, ostracods, plant fragments, and detritus. Composition of the diet was similar in both months. However, amphipods were the most important food in August, while in December amphipods, ostracods, plant fragments, and detritus were of approximately equal importance. Comparison of diel feeding periodicity and activity patterns suggests that most of the daily activity of White River springfish is related to feeding.

The White River springfish, *Crenichthys baileyi*, is endemic to several warm springs located along the course of the pluvial White River in southeastern Nevada. Abundance of White River springfish in several springs has declined in recent years as a result of habitat modifications (Courtney et al. 1985), introductions of nonnative fishes (Deacon et al. 1964, Hubbs and Deacon 1964, Courtney et al. 1985), and spread of diseases associated with introduced fishes (Wilson et al. 1966, Deacon 1979); one population became extinct because of predation by introduced largemouth bass, *Micropterus salmoides* (Deacon 1979, Williams and Wilde 1981). In general, mechanisms by which habitat modifications and introduced fishes contribute to declines in springfish abundance are not well understood. This is at least partially due to the paucity of life history information on the White River springfish; Williams and Williams (1982) provide the only description of its foods.

This paper describes the summer (August) and winter (December) diets and diel feeding periodicity of White River springfish from Hot Creek Spring, Nye County, Nevada.

Methods

Fish were collected from the springpool of Hot Creek Spring with minnow traps on 24–26 August and 29 December 1966. Contents of the stomachs of 45 fish collected in August and 21 collected in December were examined. Foods were identified and enumerated; the percentage each food contributed to the volume of the stomach contents and the percent fullness of each stomach were visually estimated. Percent frequency of occurrence and indices of absolute (AI) and relative (RI) importance were calculated following Williams and Williams (1982).

Diel feeding periodicity was determined by averaging percent fullness of the stomachs of fish collected at 2-hr intervals during 24–26 August 1966. Stomachs of five fish were examined at each 2-hr interval; empty stomachs (percent fullness = 0) were included in the analysis.

Results and Discussion

The White River springfish is an opportunistic omnivore. In Hot Creek Spring, the diet was composed of benthic invertebrates (mainly ostracods, amphipods, and gastropods), plant fragments, and detritus (Table 1), indicating that springfish foraged along the substrate and in plant cover. A similar mode of foraging is indicated in Preston Big Springs where diatoms, filamentous algae, and vascular plant fragments dominated the diet (Williams and Williams 1982).

The invertebrate fauna of Hot Creek Spring is depauperate (Brues 1932), and the diet of White River springfish showed a corresponding lack of diversity. Only five invertebrate groups were observed in stomachs of White River springfish. Intestinal tracts of fish collected in December also contained (dytiscid) coleopteran and dipteran larvae; no additional taxa were observed in intestinal tracts of fish collected in August.

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TABLE 1. Percent of stomach contents, frequency of occurrence, mean number per occurrence, and relative importance (RI) of food items in stomachs of White River springfish from Hot Creek Spring, Nevada. Sample size was 45 in August 1966 and 21 in December 1966.

	Percent of stomach contents		Frequency of occurrence		Mean number per occurrence		RI	
	August	December	August	December	August	December	August	December
Algae	4.0		18		—		6.8	
Plant fragments	10.0	39.3	35	44	—	—	10.8	24.0
Detritus	9.3	18.3	38	56	—	—	14.5	21.3
Animal remains	6.6	4.9	10	25	—	—	4.9	8.6
Gastropoda	4.9	5.3	8	6	4.0	4.0	4.0	3.2
Ostracoda	8.1	16.1	40	63	5.8	3.1	14.8	22.7
Amphipoda	50.6	15.0	73	56	3.9	2.2	38.0	20.3
Odonata	3.3		8		1.3		3.5	
Ephemeroptera	3.3		5		1.0		2.6	

There was no significant difference ($p > .10$; Mann-Whitney U-test) between August and December in fullness of the stomach; however, there were qualitative differences in the diet. Amphipods and ostracods were the most frequently consumed invertebrates and contributed 59% of the stomach contents in August, but only 31% in December. Vascular plant fragments and detritus were the most common nonanimal foods and comprised 19% of the stomach contents in August and 58% in December. The difference in diet between August and December is probably the result of decreased abundance of invertebrates in December, rather than increased availability of plant fragments and detritus, and suggests a preference for invertebrate foods.

Diel feeding periodicity and activity patterns were bimodal, with peaks in morning (0600–1000 hrs) and afternoon (1400–1600 hrs; Fig. 1). Because White River springfish are inactive at night (Deacon and Wilson 1967, Hubbs et al. 1967), feeding was at a minimum from 0200 hrs to 0400 hrs. Similarities in diel feeding periodicity and general activity suggest that most activity is related to foraging (Deacon and Minckley 1974).

The summer diet of White River springfish from Hot Creek Spring was similar in composition to that described by Williams and Williams (1982) at Preston Big Springs; however, relative importance of animal and plant foods was reversed in the two springs. Invertebrates, especially amphipods, were the most important items in the diet of springfish at Hot Creek Spring (pooled RI = 67.9); pooled RI for algae, plant fragments, and detritus was 32.1. At Preston Big Springs, pooled RIs for invertebrates and algae plus vascular plants were 32.1 and 67.9, respectively (Williams and Williams 1982).

Differences in diet between Hot Creek Spring and Preston Big Springs may result from differences in the abundance of diatoms and filamentous green algae, which Williams and Williams (1982) suggested were the preferred foods of White River springfish. The elongate digestive tract of White River springfish suggests an herbivorous nature, but does not necessarily indicate obligate or preferential herbivory. The Amargosa pupfish, *Cyprinodon nevadensis*, also has an elongate intestine (Naiman 1975). Its diet is largely composed of algae and detritus, but invertebrates are readily eaten when present (Leser and Deacon 1968, Naiman 1975).

Differences in diet are more likely related to differences in the fish communities of Hot Creek Spring and Preston Big Springs. White River springfish is the only fish present in the springpool of Hot Creek Spring; however, it is a member of a more diverse fauna at Preston Big Springs (Williams and Williams 1982). Absence of other fishes from Hot Creek Spring may allow White River springfish to assume a more carnivorous diet.

ACKNOWLEDGMENTS

B. L. Wilson performed the stomach analyses reported herein. Special thanks are due J. E. Deacon for making these data available to me and for commenting on an earlier draft of the manuscript.

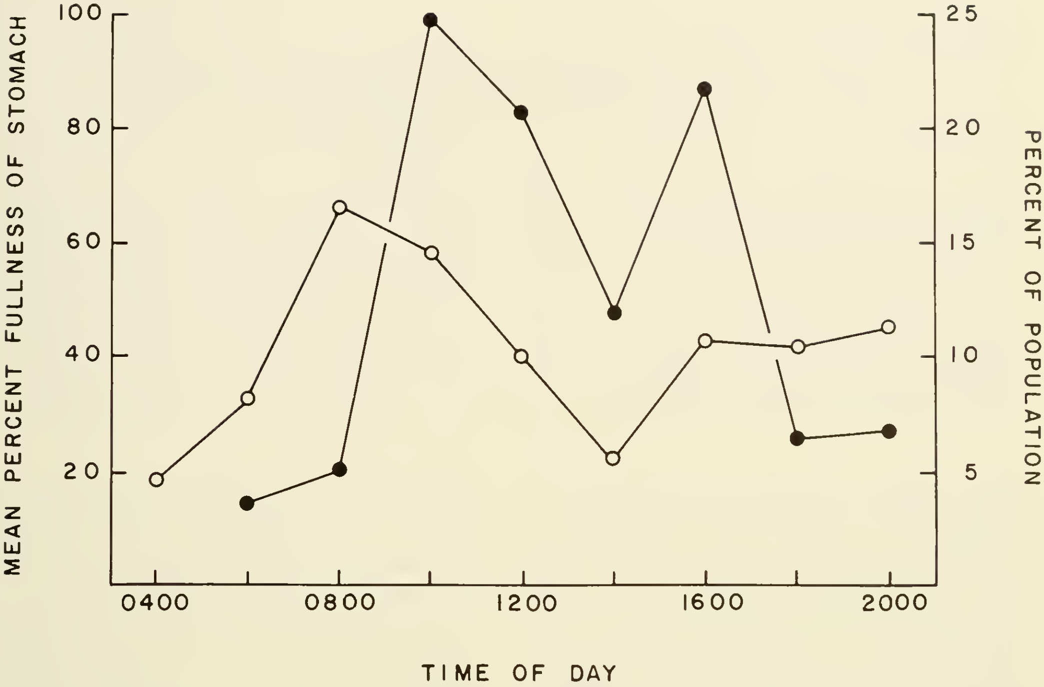

Fig. 1. Diel feeding periodicity measured as mean percent fullness of stomachs of fish captured at 2-hr intervals (open circles) and activity patterns (solid circles) of White River springfish at Hot Creek Spring, Nevada, on 24–26 August 1966. Diel activity pattern is a weighted average of patterns for 24–25 and 25–26 August 1966 and is expressed as the percent of the captured population that was taken during each interval (Deacon and Wilson 1967).

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HABITAT USE AND SELECTION AND HOME RANGES OF MERRIAM'S WILD TURKEY IN OREGON

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ABSTRACT.—Habitat use and selection by Merriam's Wild Turkeys (*Meleagris gallopavo merriami*) in Wasco County, Oregon, was studied during 1981–82. This turkey population selectively used forested cover types (such as ponderosa pine–Douglas-fir–oak, ponderosa pine–oak) characterized by a variety of structural features, species, and age classes. The population used single species forested cover types (oak, ponderosa pine) less than expected, used nonforested cover types in proportion to their availability, and avoided forested cover types with structure simplified by logging activities. The four age and sex classes had large seasonal home ranges ($\bar{x}$ = 1,615 ha); the smallest home ranges were exhibited by adult males in winter and the largest were shown by subadult males in fall. In most instances, turkeys used cover types as they were available. We suggest that structural complexity of vegetation, both within and among cover types, is an important component of habitat for Merriam's Wild Turkeys that should be considered in the evaluation of potential release sites and in habitat management plans.

The native range of Merriam's Wild Turkeys was described by Ligon (1946) as coinciding with the distribution of ponderosa pine (*Pinus ponderosa*) in Colorado, New Mexico, and Arizona. In addition, this subspecies was introduced into 10 other western states (Jonas 1966). Information on habitat use in both native and introduced ranges is sparse and limited to descriptions of roost and nest sites (Hoffman 1968, Boeker and Scott 1969, Jones 1981, Mackey 1984, Lutz and Crawford 1987a). Mackey and Jonas (1982) provided the only quantitative data on seasonal habitat use. They found that introduced Merriam's Wild Turkeys preferred forested cover types, such as ponderosa pine–oak (*Quercus garryana*) and Douglas-fir (*Psuedotsuga menziesii*), during winter, spring, and summer in Washington. There is no information on seasonal use of habitats by age and sex groups of turkeys.

Information on habitat use is essential for management of existing populations and useful in evaluation of potential release sites. Our objective was to determine habitat use and selection by a population of Merriam's Wild Turkeys that resulted from a transplant of 38 birds into Oregon from Colorado, Arizona, and New Mexico in 1961 (Mace 1965).

STUDY AREA AND METHODS

The study was conducted in southern Wasco County, Oregon, in 1981 and 1982. The 135,141-ha study area encompassed portions of Mount Hood National Forest (MHNF), the Oregon Department of Fish and Wildlife (ODFW) White River Wildlife Management Area, the Confederated Tribes of Warm Springs Reservation, and adjacent private lands. Study area boundaries were delineated by the movements of radio-marked turkeys as suggested by Porter and Church (1987). The area was located primarily within the Douglas-fir and ponderosa pine forest zones described by Franklin and Dyrness (1973). Specific cover types (Lutz and Crawford 1987b), defined according to dominant vegetation and land use practices, were mapped from LANDSAT imagery. Clearcuts were classified as either recent (< 5 years since harvest) or old (10–20 years since harvest).

Turkeys were trapped from 1 January to 5 April each year with a modified walk-in trap (Ligon 1946) consisting of four welded wire panels (1 × 3 m) and a net wire (10 × 10 cm) top. We trapped and banded 113 birds, which included 28 adults (12 F, 16 M) and 85 subadults (31 F, 54 M); 66 of these birds were equipped with radio transmitters (12 adult F, 20 subadult F, 15 adult M, and 19 subadult M). We determined age and sex of turkeys from characteristics identified by Larson and Taber (1980). We recognized two age categories of birds: subadults (8–20 months old) and adults (> 20 months old). The subadult category was based on previous work indicating that birds of the Merriam's subspecies < 2 years old were rarely involved in breeding activities (Lockwood and Sutcliffe 1985, Lutz and Crawford 1987a). Transmitters weighing 90 g and with an operational life of 12–15 months were attached with a backpack harness of rubber tubing covered by braided nylon. Transmitters contained an activity sensor that indicated when a bird remained stationary for 50–70 min. Turkeys were relocated three times weekly throughout the year to ascertain cover types used. We delineated four seasons: winter, 16 November–28 February; spring, 1 March–31 May; summer, 1 June–31 August; fall, 1 September–15 November. During radio-tracking, triangulation locations were chosen based on signal strength and the observer's experience with signal bounce. Triangulation points were plotted on habitat maps, and error polygons > 10 ha were excluded from the analysis. If a bird died within one week of capture, we assumed that the death was a result of capture stress and the bird was not used to estimate habitat use or home range. Only birds that survived an entire season were used to estimate seasonal home range sizes, but all birds that survived more than one week were used in the cover type analysis. Use of cover types was determined from 2,377 locations and based on 49 birds in winter, 32 birds in spring, 23 birds in summer, and 21 birds in fall. Home range estimates were from 32 birds during winter, 23 in spring, 22 in summer, and 21 in fall. Porter (1978) suggested that 2–3 locations/bird/week were adequate for describing home ranges. We used 18–23 locations/bird/season to estimate seasonal home ranges. Annual home range estimates were averages of seasonal home ranges. Seventeen birds were not analyzed because of radio failures (11) or capture stress (6).

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Structural characteristics of vegetation within cover types were sampled with three circular plots, each with a 10-m radius and 25 m apart. Cover values for grasses, forbs, and understory and overstory trees were estimated at four randomly selected locations within each of the three plots. A sampling frame, 0.5 m in diameter, was used to estimate ground cover, and a sighting tube (James and Shugart 1971) was used to estimate canopy cover. Indices of visual obstruction of the vegetation were obtained by traversing three 10-m transects within each plot and recording contacts with vegetation at 0.5- and 1.5-m heights.

The minimum convex polygon (Mohr 1947) and harmonic mean transformation (Dixon and Chapman 1980) methods were used to estimate seasonal home ranges for the four age and sex groups (adult and subadult males and females). Home ranges were calculated with the computer program MCPAAL (Stuwe and Blowhowiak 1986). Kruskal-Wallis rank sum test (SAS Institute, Inc. 1985: 261) was used to compare differences ($P < .10$) among seasonal home range sizes within age and sex groups of turkeys.

Bonferroni simultaneous confidence intervals (Neu et al. 1974, Byers et al. 1984) were used to test for differences between expected and observed use of the cover types. Expected values corresponded to the relative area of the cover type, and observed values were the percentage of locations of radio-equipped turkeys in the cover type. Four categories of use were defined: (1) cover type used more than would be expected by chance (selection), (2) cover type used in proportion to its availability (proportional use), (3) cover type used but less than would be expected by chance (low use), and (4) cover type not used (avoidance).

Cover type utilization was determined (1) for all birds combined on the entire study area and (2) by sex and age groups within seasonal home ranges. Preliminary analysis revealed no differences in cover types used in home ranges calculated with minimum convex polygon and harmonic mean techniques; hence, we used only results of the minimum convex polygon. To better understand use of cover types, we investigated vegetation structure (e.g., percent cover, density) within cover types by comparison of location sites with random (available) sites. A random sample of locations ($n = 337$) was used for the vegetation structure utilization analysis. Random sites were sampled in each cover type to provide information on "available" vegetation structure. Differences in vegetative structure between locations used by turkeys and random sites were tested with multivariate analysis of variance (MANOVA; Hull and Nie 1981:1).

TABLE 1. Annual selection of cover types used by Merriam's Wild Turkeys, Wasco County, Oregon, 1981–82.

Cover type	Available	Used	Bonferroni
Oak[a]	0.246	0.169	0.148–0.189
Ponderosa pine[a]	0.178	0.053	0.048–0.065
Mature mixed conifer[a]	0.142	0.169	0.148–0.189
Ponderosa pine–Douglas-fir–oak[a]	0.125	0.179	0.158–0.199
Ponderosa pine–oak[a]	0.095	0.146	0.126–0.165
Thinned mixed conifer[a]	0.078	0.146	0.126–0.165
Young mixed conifer[a]	0.077	0.098	0.081–0.114
Grain	0.046	0.002	0–0.004
Rangeland[a]	0.006	0.028	0.019–0.036
Shelterwood	0.006	0	
Old clearcut[a]	0.006	0.002	0–0.004
Irrigated pasture	0.003	0.002	0–0.049
Mixed deciduous	0.002	0.002	0–0.004
Recent clearcut	0.001	0	

[a] Significant at $P < .05$.

RESULTS AND DISCUSSION

Habitat Use on the Study Area

Major cover types available on the study area included oak (24.6%), ponderosa pine (17.8%), mature mixed conifer (14.2%), and ponderosa pine–Douglas-fir–oak (12.5%). Turkeys used 12 of 14 cover types, of which 6 were selected, 3 were used in proportion to their availability, 3 were used less than expected, and 2 were avoided (Table 1). Five of the 6 most frequently used forested cover types were selected by turkeys (Table 1).

In all cover types selected by turkeys, multiple species and age classes characterized the shrub, understory, and overstory strata (Lutz and Crawford 1987b). Mackey and Jonas (1982) also found that a multispecies cover type, pine-oak, was selected during winter, spring, and summer by Merriam's Wild Turkeys in Washington. Merriam's Turkeys often were associated with ponderosa pine (Ligon 1946), but the ponderosa pine cover type was used less than expected on our study area. Both cover types that were dominated by single species, ponderosa pine and oak, were used less than expected on our study area. The permanent water sources often adjacent to irrigated pastures and moist, mixed deciduous cover types probably influenced use by turkeys. Ligon (1946) reported that water was a critical factor affecting the distribution of Merriam's Wild Turkeys. Poor water distribution, especially among the drier sites that were often dominated by ponderosa pine, could explain why turkeys used this cover type less than expected. Grain fields, composed largely of harvested winter wheat, were used during winter for foraging. This cover type may be important during winters with severe weather. Cornfields in the Midwest were used by Eastern Wild Turkeys as winter foraging sites during winters with deep snow (Porter 1978) and during years of mast failures (Kurzejeski et al. 1987). Recent clearcuts and shelterwoods were avoided by turkeys; both cover types resulted from logging activities that substantially simplified habitat structure.

We compared structural characteristics between sites used by turkeys and randomly sampled sites (Table 2). Initially, we combined all cover types and found that greater forb cover and understory density and lower overstory density and obstruction of vision at 0.5 m characterized sites used by turkeys. Individual cover types selected were characterized by either greater forb densities or by a higher density of woody plants (shrubs, understory, and overstory). Grass was identified as an important food item for turkeys (Mackey and Jonas 1982), and food availability was proposed as an influence on home range size. The preponderance of forbs in cover types used by turkeys on our study area may indicate marginal habitat quality. The higher density in cover types used by turkeys possibly afforded protection from predation, a major cause of mortality. Jonas (1966) reported that dense, pole-size stands of ponderosa pine were used frequently as escape cover by Merriam's Wild Turkeys. Quantitative descriptions of habitat used by Eastern Wild Turkeys (Gwaltney 1977, Hopkins 1981) also identified vegetation density as an important factor determining utilization of cover types.

TABLE 2. Values of structural features in cover types used and selected by Merriam's Wild Turkey, Wasco County, Oregon, 1981–1982.

	Structural feature						
Cover type	Forb cover (%)	Grass cover (%)	Shrub density (#/ha)	Understory density (#/ha)	Overstory density (%)	Obstruction of vision @ 0.5 m	Obstruction of vision @ 1.5 m
Oak (n = 33)	4	18	541	343[a]	490[b]	1.0	0.9
Ponderosa pine (n = 47)	6[a]	10	656[a]	657	198	1.4	1.3
Mature mixed conifer (n = 65)	7	6[a]	617	745[a]	201	1.3[b]	1.2[b]
Ponderosa pine–Douglas-fir–oak (n = 70)	7	7	1075	777[a]	259	2.0	1.2
Ponderosa pine–oak (n = 75)	6	14	975[a]	500[a]	232	0.9	0.8
Thinned mixed conifer (n = 17)	7[a]	3	1152	304	313	1.5	1.1
Young mixed conifer (n = 30)	8[a]	4	504	721	196	1.0	1.9
Combined cover types (n = 337)	9[a]	18	709	656[a]	217[b]	1.3[b]	1.1

[a] Value significantly ($P < .05$) greater than value from random site.
[b] Value significantly ($P < .05$) less than value from random site.

Home Ranges

Home ranges were largest in spring (2,575 ha), intermediate in fall (1,738 ha) and summer (1,509 ha), and smallest in winter (636 ha) (Table 3). Mackey (1982) reported a similar trend in seasonal home range size of Merriam's Turkeys in Washington, but sizes were substantially smaller (winter 63 ha, spring 140 ha, summer 77 ha). Subadult females in spring had the largest home ranges (4,213 ha), and adult males in winter had the smallest home ranges (347 ha). Differences among turkey home range sizes were detected in three of four seasons; only spring home range sizes were not statistically different. Our estimates of seasonal home range size also were larger than the range of 65 to 683 ha reported for Eastern Wild Turkeys (Brown 1980). Wigley et al. (1986) reported large seasonal home ranges ($\bar{x}$ = 1,295 ha) for Eastern Wild Turkeys in the Ouachita Mountains in Arkansas and suggested that the large home range size was partly a response to declining habitat quality. Lutz (1987) found that turkey mortality indices were related to home range size ($r^2 = .81$, $P < .05$) and suggested that mobility and mortality were related.

Habitat Use Within Home Ranges

There was little selection seasonally of cover types among age and sex groups of turkeys (Table 4). Six to eight cover types were used by turkeys during each season (Table 4); three, including ponderosa pine–Douglas-fir–oak, mature mixed conifer, and oak, accounted for > 50% of the locations. In only three instances was there selection: adult females selected rangeland in winter and thinned mixed conifer in spring, and subadult females selected ponderosa pine during summer. In all other cases, turkeys used cover types seasonally in proportion to their availability. Because Merriam's Wild Turkeys rely heavily on grass and grass parts (Mackey and Jonas 1982) as food, rangeland was probably an important foraging site, especially during winter. Thinned mixed conifer was used almost exclusively as nesting habitat by adult females in spring (Lutz and Crawford 1987a). Ponderosa pine was selected only by subadult females in summer and coincided with a time of high mortality (Lutz 1987), but we do not know if this selection was causal or coincidental.

Lack of selection within home ranges by individual age and sex groups contrasted with

TABLE 3. Size (ha) of seasonal home ranges for four age and sex groups of Merriam's Wild Turkey, Wasco County, Oregon, 1981–1982.

	Season[a]			
Age/sex	Winter	Spring	Summer	Fall
Adult male (n = 6)	347 (43)	1,655 (425)	1,469 (510)	881 (83)
Subadult male (n = 11)	988 (298)	2,345 (247)	1,772 (388)	2,381 (582)
Adult female (n = 12)	288 (36)	2,085 (395)	1,307 (321)	1,273 (589)
Subadult female (n = 8)	921 (491)	4,213 (392)	1,488 (981)	2,417 (269)
$\bar{x}$	636	2,575	1,509	1,738

[a] Mean (standard error)

TABLE 4. Use (%) of cover types in seasonal home ranges by four age and sex groups of Merriam's Wild Turkeys, Wasco County, Oregon, 1981–1982.

Season		Cover type[b]										
	Age/sex[a]	OCC	IP	RA	OA	PP–OA	YMC	MMD	TMC	P–D–O	MMC	PP
Winter												
	AM	2	2	0	40	5	12	0	6	27	5	0
	SM	0	0	5	29	11	13	0	13	14	15	0
	AF	0	0	8[c]	19	17	8	0	10	6	32	0
	SF	0	0	7	25	10	16	0	12	15	15	0
Spring												
	AM	0	0	0	21	12	17	0	8	21	15	5
	SM	0	0	1	13	18	9	0	15	18	24	2
	AF	0	0	2	8	15	9	0	25[c]	15	23	4
	SF	0	0	3	10	15	7	0	18	20	16	11
Summer												
	AM	0	0	0	24	15	6	0	8	21	14	11
	SM	0	0	0	13	14	11	1	20	18	14	9
	AF	0	2	1	13	12	10	1	14	25	12	9
	SF	0	0	1	8	8	8	0	14	7	17	35[c]
Fall												
	AM	0	0	3	13	26	11	0	9	24	14	0
	SM	0	0	0	21	24	10	0	4	19	17	4
	AF	0	0	10	28	17	4	1	8	19	13	1
	SF	0	0	8	25	13	6	0	15	23	4	3

[a] AM = adult male, SM = subadult male, AF = adult female, SF = subadult female.

[b] OCC = old clearcut, IP = irrigated pasture, RA = rangeland, OA = oak, PP–OA = ponderosa pine–oak, YMC = young mixed conifer, MMD = moist mixed deciduous, TMC = thinned mixed conifer, P–D–O = ponderosa pine–Douglas-fir–oak, MMC = mature mixed conifer, PP = ponderosa pine.

[c] Indicates a difference at the .05 level of significance.

apparent strong selection for habitats on a study area basis and suggested that selection processes occurred only at the higher level (i.e., study area). As an example of levels of selection, Johnson (1980) addressed the concept of the hierarchical nature of selection and suggested that the home range of an animal is indicative of second-order selection. He cautioned that comparing usage values to availabilities within the home range (third-order) could be misleading.

CONCLUSIONS

Both use and selection of cover types indicated that a variety of cover types were used by Merriam's Wild Turkeys on the study area. Cover types that were both used and selected, mature mixed conifer, ponderosa pine–Douglas-fir–oak, ponderosa pine–oak, thinned mixed conifer, young mixed conifer, and rangeland, were probably important cover types for turkeys.

Korschgen (1967) reported that most successful introductions and reintroductions of Merriam's Wild Turkeys occurred in ponderosa pine–grassland associations. Turkeys in this study used ponderosa pine much less than expected; this may have been related to the distribution of water. Apparently, an array of forested cover types rather than a single type provided the elements necessary to maintain this turkey population. Large home ranges suggested that turkeys made substantial movements to fulfill life history needs. This was interpreted as evidence that this area represented relatively poor quality habitat. Both cover type availability and juxtaposition likely influence habitat quality, but investigating the juxtaposition of cover types was beyond the scope of our work. We suggest that structural complexity and plant species and age–class diversity, both within and among cover types, are important characteristics of potential release sites and also could serve as a habitat management goal for extant Merriam's Wild Turkey populations. Our work confirmed that turkeys were largely generalists in their use of cover types.

ACKNOWLEDGMENTS

Funding for the project was provided by MHNF, ODFW, and Oregon State University Computer Center. We thank R. D. Denney (ODFW) and D. P. Longrie (MHNF) for their assistance in administering the project, and D. R. Lockwood, New Mexico Game and Fish Department, who provided unpublished data. R. G. Anthony, W. H. Emmingham, W. C. Krueger, G. L. Zimmerman, and K. M. Kilbride reviewed earlier drafts of this manuscript. A. C. Heath assisted with fieldwork. This is Technical Publication 8320 of the Oregon Agricultural Experiment Station.

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GERRIDAE (WATER STRIDERS) OF IDAHO (HETEROPTERA)[1]

R. C. Biggam[2] and M. A. Brusven[2]

Abstract.—A biosystematic study on the Gerridae of Idaho was undertaken to clarify and describe the taxonomy, species distribution, and biology of this aquatic hemipteran family. Three genera and 7 species were collected in the state. Keys to three genera and 10 species are provided. General descriptions, diagnoses, and distributional ranges are given for species occurring within and adjacent to Idaho.

Special interest in aquatic and subaquatic Heteroptera by the authors and recently published papers on the Gerridae of Montana (Roemhild 1976) and Oregon and Washington (Stonedahl and Lattin 1982) prompted this taxonomic study on the Gerridae of Idaho. The ubiquitous nature, conspicuous habits, predaceous activities, and nutritive value of gerrids to higher trophic levels make them an important group in aquatic and semiaquatic ecosystems.

The purposes of this study were to determine the distributions of species occurring in Idaho, clarify taxonomic differences between related species occurring in or adjacent to the state, provide a diagnostic key for the identification of species, and provide information on habitat affinities. Three genera and seven species of Gerridae are recorded in the state.

Classification and Distribution

Approximately 488 species of Gerridae in 55 genera occur throughout the world (Andersen 1982). Five subfamilies were recognized by Hungerford and Matsuda (1960) and eight by Andersen (1975, 1982); two occur in Idaho and the Pacific Northwest (Gerrinae and Trepobatinae).

The family Gerridae is worldwide in distribution except for the polar regions. Gerrids live on the surfaces of rivers, mountain streams, and warm ponds (Fairbairn 1985a), lakes, reservoirs, irrigation canals, and hot springs (Calabrese and Tallerico 1982), road puddles, ditches, sinkhole ponds, marshes, and swamps (Herring 1950, 1951), saline lakes (Scudder 1969, 1971), brackish coastal waters (Vepsäläinen 1973, Andersen 1975, Cobben 1960), and the open ocean (Andersen and Polhemus 1976). Five species of the genus *Halobates* have been collected hundreds of miles from the nearest land (Cheng 1974), making them one of the few insects to successfully occupy the open ocean. Vepsäläinen (1973), Calabrese (1977), and Spence and Scudder (1980) found that gerrids display habitat preferences. Strict habitat association is the most important factor in ecological species separation and coexistence (Spence and Scudder 1980, Spence 1983).

Biology and Life History

Gerrids are opportunistic predators (Jamieson and Scudder 1977) on other insects of the neuston community and terrestrial invertebrates that fall into the water. They are also known to feed on fruits and berries (Riley 1918). Live prey are preferred, but scavenging and cannibalism are probably necessary for some to survive. Coastal gerrids may feed on windblown terrestrial insects found on the sea (Andersen and Polhemus 1976). Ocean-going *Halobates* feed on coelenterates (Savilov 1967). Cannibalism occurs in most species and is usually the result of overcrowding, food shortage, or vulnerability during molting (Riley 1922a, 1922b, 1925, Stonedahl and Lattin 1982). Gerrids detect their prey and mates by orientation to surface waves caused by the object of intent (Murphy 1971a, 1971b, 1971c, Weber 1930, Wilcox 1972, 1979, Lawry 1973). The prey is quickly grasped by the raptorial forelegs, after which the cutting, mandibular stylets of the forward-extended rostrum are inserted into the prey (Cobben 1978). These stylets also serve in the transfer of enzymatic secretions into the prey and the extraction of the prey's body fluids (Cheng 1967a, 1974).

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[1] Approved by the director of the Idaho Agricultural Experiment Station as Research Paper #8876.

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Gerrids have hemimetabolous or gradual development; the immature stage is a nymph. Eggs are attached to submerged vegetation or other substrates either singly or in clusters (Hungerford 1920, Cobben 1968, Andersen and Polhemus 1976). One European species, *Gerris najas* De Geer, attaches its eggs to lake bottom substrates (Brinkhurst 1960), whereas members of the subfamily Rhagadotarsinae insert their eggs directly into plant tissue (Silvey 1931). The eggs, usually white when laid, turn to amber with age and range in size from 1.0 × 0.33 mm to 1.6 × 0.5 mm (Herring 1961). The eggs usually hatch within 14 days (Torre-Bueno 1917a, 1917b, Hungerford 1920, Hoffman 1924, Bobb 1951, Herring 1961, Cheng 1967b). An egg burster is used by the first instar nymph to escape from the chorion (Hungerford 1920, Cobben 1968). The newly hatched nymphs make their way to the surface, break the surface tension, and begin life on the water's surface. Depending on environmental factors, one to six generations per year have been noted (Torre-Bueno 1917a, Hoffman 1924, Cheng 1967b, Cheng and Fernando 1970, Bobb 1974, Vepsäläinen 1974b, 1974c, Callahan 1974, Polhemus and Chapman 1979, Spence and Scudder 1980). The nymphs have five instars or molts and require 21 to 44 days to achieve adulthood (Penn and Goldsmith 1950, Bobb 1951, Herring 1961).

Spence et al. (1980b) reported that temperature is very important in development. They observed several species basking underwater during low air temperatures, presumably to increase gonad development (1980a). The nymphs are similar in appearance to the adults except in size, body proportion, near absence of external genitalic structures, lack of scent glands, and presence of only one tarsal segment per leg. After ecdysis via a Y-shaped suture on the thorax (Cheng 1967b), the adults remain teneral for several days, thus leaving themselves vulnerable to predation and cannibalism (Andersen 1973).

Wing polymorphism in the adult stage is prevalent in most species (Brinkhurst 1959, 1961, 1963, Vepsäläinen 1971a, 1971b, 1974a, 1974b, Andersen 1973, Järvinen 1976, Järvinen and Vepsäläinen 1976) where apterous to macropterous forms can occur. Apterous populations usually indicate a stable population and habitat. Macropterous populations are common in unstable or confined habitats such as ponds or lakes. In populations with multiple generations, early apterous generations often produce macropterous individuals for population dispersion (Brinkhurst 1963). Macropterous forms usually overwinter as adults and reproduce the following season. Occasionally, brachypterous and micropterous forms of the same species may occur together, the result of population density, climatic changes, and/or habitat instability. Vepsäläinen (1971a, 1971b) observed that an environmental switching mechanism caused by day length, temperature, and illumination rhythm is the probable cause of the varying wing lengths from one generation to the next in bivoltine or trivoltine populations.

Gerrid flight activity has been reported by Riley (1920), Leech (1970), Callahan (1974), and Spence and Scudder (1980). Riley (1925) lists food deficiency, drought, and overcrowding as important factors influencing flight. Overcrowding can also result in compensatory upstream dispersal (Fairbairn 1985b). Shortened day lengths during larval development induce diapause (Vepsäläinen 1971b, 1974a, 1974d). Lee et al. (1975) reported that triglycerides were metabolized during hibernation in *G. remigis* Say.

Gerrids are fed upon by frogs (Drake 1914, Torre-Bueno 1917b, Riley 1925, Callahan 1974), fish and *Dytiscus* beetles (Riley 1925), ducks (McAtee 1918, Mabbot 1920, Anderson 1932), shorebirds (Wetmore 1925), swallows (Beal 1918), trout (Callahan 1974), and hedgehogs (Obrtel and Holisova 1981). The senior author observed *Grylloblatta campodeiformis* Walker (Orthoptera: Grylloblattidae) feeding on *Gerris remigis* Say. Cooper (1984), although never observing trout actually feeding on gerrids in the wild, reported fish readily taking experimentally disabled specimens. Some gerrids will attempt to escape predation by feigning death (Essenberg 1915, Riley 1921, Callahan 1974). Gerrids can inflict a painful bite with their beak, and the pain can be long lasting.

TABLE 1. The taxa, habitats, trophic relationships, and seasonal occurrences of the Gerridae of Idaho.

Taxa	Habitat	Trophic[1] relationships	Seasonal occurrence	
			In Idaho	In literature
Gerris				
buenoi Kirkaldy	Lentic (Lotic)	Predators–piercers; scavengers	Mar–Sep	Mar–Sep
comatus Drake & Hottes	Lentic (Lotic)	Predators–piercers; scavengers	*	May–Sep
gillettei Lethierry & Severin	Lentic	Predators–piercers; scavengers	Apr–Aug	Apr–Oct
incognitus Drake & Hottes	Lentic (Lotic)	Predators–piercers; scavengers	Mar–Sep	Feb–Nov
incurvatus Drake & Hottes	Lentic	Predators–piercers; scavengers	Mar–Oct	Mar–Oct
marginatus Say	Lentic (Lotic)	Predators–piercers; scavengers	*	Mar–Oct
pingreensis Drake & Hottes	Lentic	Predators–piercers; scavengers	*	May–Sep
remigis Say	Lotic (Lentic)	Predators–piercers; scavengers	Jan–Dec	Jan–Dec
Limnoporus		Predators–piercers		
notabilis Drake & Hottes	Lentic (Lotic)	Predators–piercers	Mar–Oct	Mar–Sep
Metrobates		Predators–piercers		
trux infuscatus Usinger	Lotic	Predators–piercers	Jul–Sep	Jul–Sep

[1] Polhemus (1984).

*Not recorded in Idaho, but may occur in state.

Flagellate protozoans (Trypanosomes) (Poisson 1957, Wallace et al. 1960), nematodes (Poisson 1957), and parasitic Hymenoptera (Usinger 1956) in the families Mymaridae (*Caraphractus cinctus* Walker & *Anaphes gerrisophaga* [Doutt] Gordh 1979) and Scelionidae (*Tiphodytes gerriphagus* [Marchal] Muesebeck 1979) are reported as being endoparasites of gerrid eggs. Larvae of certain Hydracarina (water mites) are known ectoparasites of gerrids (Torre-Bueno 1917a, Polhemus and Chapman 1979). Maier (1977) and Schaefer (1978) reported cleptoparasitic interactions between hydrometrids and gerrid prey where the hydrometrid obtained a meal from a gerrid's prey by simultaneously feeding on it.

Life history studies have been reported in the literature for many species. Confusion between similar species has likely led to inaccurate accounts for some (Drake and Harris 1934).

A general overview of habitat, trophic relationships, and seasonal occurrence for the Idaho species is given in Table 1. General distribution is discussed for each species.

General Description and Diagnosis

Members of the family Gerridae, known to many as water striders, pond skaters, or wherrymen, are small- to medium-sized insects (6.65–20.0 mm) with narrow, elongate bodies and long legs. The head is shorter than the pronotum and mesonotum combined. A four-segmented, filiform antenna is inserted on either side of the head behind the large, rounded, compound eyes; ocelli are absent. The rostrum or beak is four-segmented. The thorax is variable according to the degree of wing development. Apterous, brachypterous, and macropterous forms occur in many species. The forelegs are short and raptorial, whereas the middle and hind legs are long and slender and have two tarsal segments present in the adults; the nymphs have one segment. Tarsal claws are preapical. The procoxae are remote from the meso- and metacoxae. A median scent gland opening on the metasternum, the omphalium, is found in most gerrids but is absent in the subfamilies Rhagadotarsinae and many Trepobatinae. A velvety gray to dark brown pile of hydrofuge hairs covers most of the body. Cheng (1973) found two types of hairs in *Halobates:* (1) macrotrichia (long, slender hairs) and (2) microtrichia (hooklike hairs). Andersen and Polhemus (1976) reported that most water striders have hairs similar to those found by Cheng.

The gerrids differ from the families Corixidae, Nepidae, Belostomatidae, Ochteridae, Gelastocoridae, Naucoridae, Notonectidae, and Pleidae in having the antennae longer than the head. Gerrids differ from Saldidae in having the hind coxae smaller, more conical or cylindrical, and freely rotatory as compared to saldids, which have transverse, fixed coxae. Gerrids differ from the Macroveliidae, Mesoveliidae, Hebridae, and Hydrometridae in having their tarsal claws inserted preapically on the last tarsal segment, a character shared with the family Veliidae. Although gerrids are similar to veliids in general appearance, they differ markedly in the length of the hind femur. In Idaho veliids, the hind femur scarcely, if at all, surpasses the tip of the abdomen, while in gerrids, the hind femur greatly exceeds the apex of the abdomen. Also, the middle legs are attached much closer to the hind legs in the gerrids; veliids have the middle legs attached approximately midway between the front and hind legs. Gerrids have a single scent gland opening on the metasternum; veliids have two scent gland openings, delineated by a pair of channels that run laterad and end anterior to the hind coxae. The most reliable criterion for separating these two families is the sclerotizaton of the vesica of the aedeagus in gerrids and its absence in veliids (Polhemus and Chapman 1979, China 1957). Female gerrids have the second gonocoxites absent, while veliids have them well developed (Scudder 1959). The Idaho gerrids can easily be separated from the veliids by the absence of the metathoracic scent gland channels.

Key to the Species of Adult Idaho Gerridae

1. Inner margins of eyes sinuate or concave posteromedially in dorsal view (Fig. 1); first antennal segment shorter than remaining three combined; abdomen elongate, segments not dorsoventrally flattened; ground color black to brown with various gold markings 2

— Inner margin of eyes convexly rounded posteromedially in dorsal view (Fig. 2); first antennal segment longer than remaining three combined; abdomen short, dorsoventrally flattened, appearing atrophied; ground color grey with black markings .... *Metrobates trux infuscatus* Usinger

2(1). Length of first antennal segment less than segments two and three combined; males with abdominal sternite six evenly emarginate posteriorly (Fig. 3); female connexival spines of abdominal segment six reaching to or beyond middle of last genital segment (Fig. 4) .... *Limnoporus notabilis* (Drake & Hottes)

— Length of first antennal segment equal to or greater than segments two and three combined; male with abdominal sternite six sinuately emarginate posteriorly (Figs. 5, 9, 12, 17); female connexival spines of abdominal segment six not reaching middle of last genital segment 3

3(2). Species large (exceeding 12 mm); abdominal sternite seven of male with medial keel prominent and elevated (Fig. 5) .... *Gerris (Aquarius) remigis* Say

— Species small (under 12 mm); abdominal sternite seven of male with medial keel slightly prominent (Figs. 12, 17) or absent (Fig. 9)...... 4

4(3). Pronotum entirely dark, lacking yellowish to russet brown anterolateral stripes immediately posterior to compound eyes; if pale stripes present, then basal three-fourths of first antennal segment with inner and outer surfaces having narrow, longitudinal, dark stripes (Fig. 7)... 8

— Pronotum with yellowish to russet brown anterolateral stripes immediately posterior to compound eyes (Fig. 6); basal three-fourths of first antennal segment entirely black (Fig. 8) . . . 5

5(4). Abdominal sternite seven of male as long as broad; posterior, median notch on abdominal sternite six subrectangular (Fig. 9); female with posterolateral angles of tergite six not produced into distinct connexival spines; abdominal sternite seven subrectangular, the posterior edges of each valve obtuse (Fig. 10). . . . . *Gerris (Gerris) buenoi* Kirkaldy

— Abdominal sternite seven of male longer than broad; posterior, median notch on abdominal sternite six evenly rounded (Figs. 12, 17); female with posterolateral angles of tergite six produced into distinct connexival spines; abdominal sternite seven triangular, the posterior edges of each valve acute (Fig. 11) 6

6(5). Abdominal sternite seven of male with longitudinal rows of long hairs on either side of ventral keel (Fig. 12); pale area along dorsolateral margins of abdominal sternites extending the length of the abdomen (Fig. 13). . . . . *Gerris (Gerris) incognitus* Drake & Hottes

— Abdominal sternite seven of male lacking long hairs on either side of ventral keel; pale area along dorsolateral margins of abdominal sternites only on segments five, six, and seven (Fig. 14) 7

7(6). Corners of abdominal tergites with tufts of silvery pubescense (visible only on dry, degreased specimens) (Fig. 15); connexival spines of female curving slightly inward and upward . . . . *Gerris (Gerris) gillettei* Lethierry & Severin

— Corners of abdominal tergites without tufts of silvery pubescence; connexival spines of female pointed almost vertically . . . . *Gerris (Gerris) pingreensis* Drake & Hottes[3]

8(4). Disc of pronotum with uniform, minute, gold specks not interrupted by two longitudinal bands of reflective, silvery setae (visible only on dry, degreased specimens); connexial spines of female strongly curved inward, not reaching apex of abdominal tergite seven . . . . *Gerris (Gerris) incurvatus* Drake & Hottes

— Disc of pronotum with uniform, minute, gold specks interrupted by two longitudinal bands of reflective, silvery setae (Fig. 16) (visible only on dry, degreased specimens); connexival spines of female not strongly curved inward, reaching apex of abdominal tergite seven 9

9(8). Abdominal sternite seven of male with distinct, circular, raised tufts of hair on either side of median, ventral keel (Fig. 17); connexival spines of female strongly incurved with apices clothed with stiff hairs (Fig. 18) . . . . *Gerris (Gerris) comatus* Drake and Hottes[4]

— Abdominal sternite seven of male lacking distinct tufts of hair on either side of median, ventral keel; connexival spines of female not strongly incurved with apices lacking stiff hairs (Fig. 19) . . . . *Gerris (Gerris) marginatus* Say[3]

Subfamily Gerrinae

Andersen (1975) recognized one of two tribes (the Gerrini) and four genera in North America. The genera *Limnoporus* and *Gerris* are the only representatives of this subfamily and of the tribe Gerrini in Idaho.

Genus *Gerris* Fabricius

Gerris Fabricius, 1794. Entomol. Syst. 4: 188. Type species: *Cimex lacustris* Linnaeus, 1758. Designated by Latreille, 1810.

Aquarius Schellenberg, 1800. Das geschlect der Land und Wasserwanzen, p. 25 (= subgenus).

Hygrotrechus Stål, 1868. Ofvers. K. Vet.-Akad. Forh 25: 395 (= *Aquarius*).

Limnotrechus Stål, 1868. Ofvers, K. Vet.-Akad. Forh 25: 395.

Ures Distant, 1910. Fuana British India, Rhynchota 5: 149.

Gerriselloides Hungerford & Matsuda, 1958. Entomol. News 69: 259 (= subgenus).

This is the most common and widely distributed genus of Gerridae in the world. Fifteen species are known from the Nearctic region, and nine were recorded from Idaho by Drake and Harris (1934). One of these was transferred to the genus *Limnoporus* by Andersen (1975). Two others, *G. remigis* Say and *G. nyctalis* Drake & Hottes, are combined under the former name in this paper following the suggestion of Stonedahl and Lattin (1982). *Gerris marginatus* Say, recorded from Idaho by Drake and Harris (1934), is believed not to occur west of the Continental Divide except for a single specimen collected in western Montana. An additional three species are included in the key as possibly occurring in the state. Sprague (1967), Scudder and Jamieson (1972), and Calabrese (1974a) described the nymphs of most North American species.

Gerris (Aquarius) remigis Say

Figs. 1, 5

Gerris remigis Say, 1832. Descriptions of new species of heteropterous Hemiptera of North America, New Harmony, Indiana. Page 35 *in* The complete writings of Thomas Say on the entomology of North America. J. L. LeConte, ed. Vol I. 362 pp. Bailliere Brothers, New York. (Types destroyed).

Gerris orba Stål, 1859. K. Sven. Fregatten Eugenies Resa Omkring Jordon, Zool. 4: 264.

Hygrotrechus robustus Uhler, 1871a. Amer. J. Sci. (3)1: 105.

Gerris remigis caloregon Calabrese, 1974b. Entomol. News 85: 27.

The large size of this transcontinental species (length 11.0–16.6 mm, width 3–4 mm)

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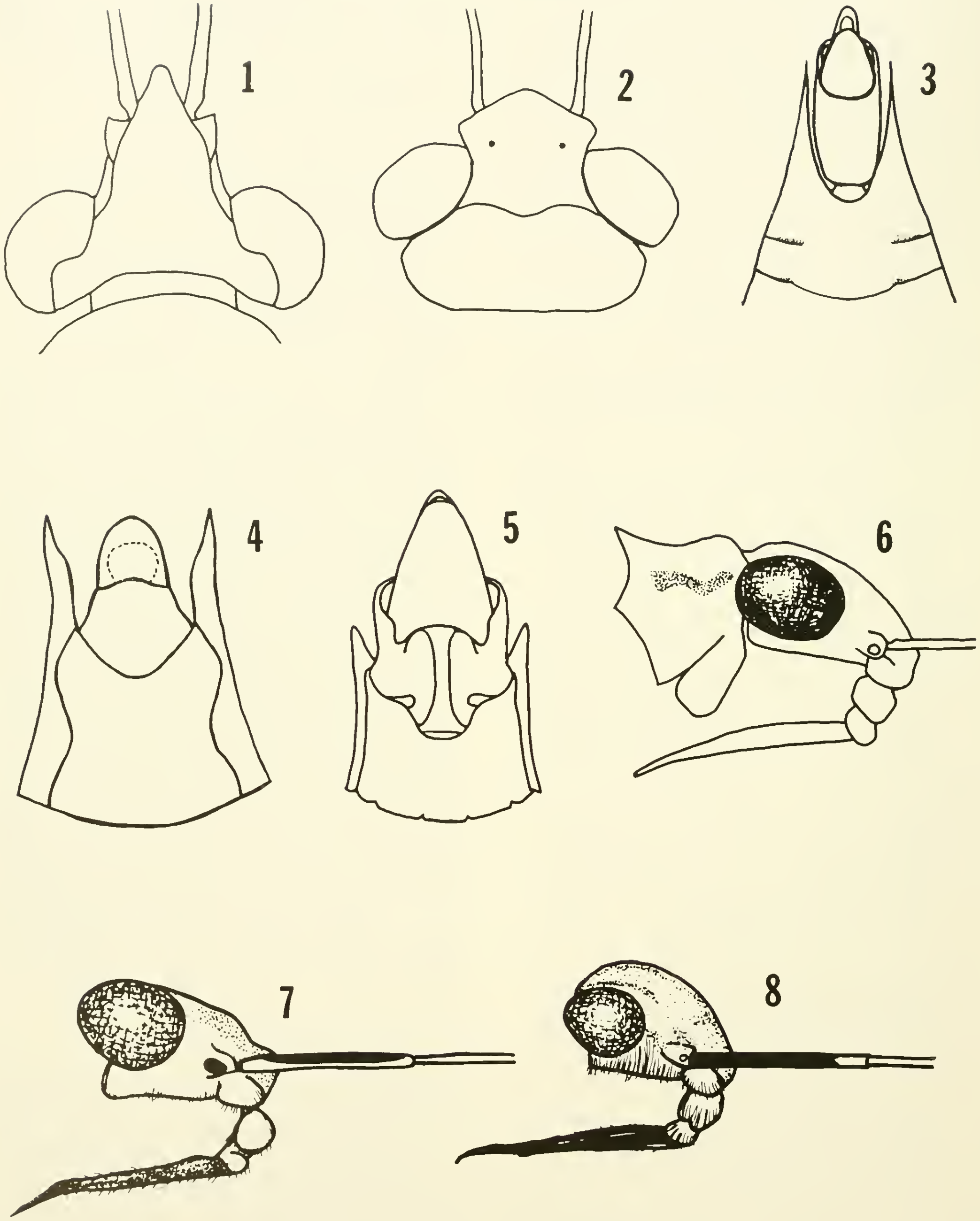
[3] Reported from Idaho by Drake and Harris (1934), but were likely misidentified.

[4] Not recorded from Idaho.



Figs. 1–8. 1, *Gerris remigis*, dorsal view of head; 2, *Metrobates trux infuscatus*, dorsal view of head; 3, *Limnoporus notabilis*, ventral view of male abdominal apex; 4, *Limnoporus notabilis*, ventral view of female abdominal apex; 5, *Gerris remigis*, ventral view of male abdominal apex; 6, *Gerris incurvatus*, lateral view of head and pronotum; 7, *Gerris buenoi*, lateral view of head; 8, *Gerris incognitus*, lateral view of head.

makes it easy to distinguish in the field from other species of *Gerris*. This species is more robust and shorter than members of the genus *Limnoporus*. It is the most abundant and widely distributed species of gerrid in the state. Macropterous and apterous forms have been collected in Idaho. Brachypterous forms occur rarely in the Pacific Northwest (Stonedahl and Lattin 1982), but remain uncollected in Idaho. Torre-Bueno (1917a), Scudder and Jamieson (1972), and Calabrese (1974a) described the nymphs.

Geographic range.—Reported from the 48 contiguous states, Canada, Mexico, and Guatemala (Drake and Harris 1934). As defined here and by Stonedahl and Lattin (1982), *G. remigis* includes several forms from different regions of North America. Several of these forms have been described as distinct species and subspecies: *Gerris orba* Stäl (1859) from San Francisco, California, and *G. remigis caloregon* Calabrese (1974b) from California and Oregon. In addition, *Gerris nyctalis* Drake & Hottes (1925a) was described from the U.S. National Park near Estes Park, Colorado, which is in the Rocky Mountains east of the Continental Divide. Michel (1962) reported a *remigis*-like form in Arizona, Texas, and Virginia. He claimed definite differences in internal genitalia in eastern vs. western forms, but apparently without examining type material or specimens from the type locality. Drake and Harris noted the occurrence of *G. nyctalis* in lakes at high elevations in the Rocky Mountain regions, including Idaho. An intensive study will be necessary to determine the true taxonomic status of these forms. In this paper we will call this polymorphic species *Gerris remigis* Say, as proposed by Stonedahl and Lattin (1982).

Idaho records.—Specimens have been collected on the surfaces of ponds, lakes, reservoirs, creeks, and rivers in 33 counties: Ada, Benewah, Bingham, Blaine, Boise, Bonner, Bonneville, Boundary, Butte, Camas, Canyon, Cassia, Custer, Elmore, Franklin, Fremont, Gooding, Jefferson, Kootenai, Latah, Lemhi, Lewis, Lincoln, Madison, Minidoka, Nez Perce, Oneida, Payette, Shoshone, Twin Falls, Valley, and Washington. Adults have been collected every month of the year except November, and nymphs have been collected from May through November.

Gerris (Gerris) buenoi Kirkaldy

Figs. 7, 9, 10

Gerris buenoi Kirkaldy, 1911. Entomol. News 22: 246. Lectotype, macropterous female: Fort Collins, Colorado (CAS), designated by Menke and Polhemus (1973).

The broad, rectangular notch at the apex of sternum seven of the male and the female's lack of spinelike, lateral prolongations on tergum six, combined with the presence of the anterolateral, pale, pronotal stripe and its small size (length 6.5–8.2 mm, width 1.3–1.6 mm) separate this species from other Idaho gerrids. Only macropterous and brachypterous forms have been collected in Idaho and the Pacific Northwest.

Geographic range.—Transcontinental in southern Canada and the northern United States from British Columbia east to New Jersey (Torre-Bueno 1911) and Massachusetts (Parshley 1916), southward into California (Polhemus and Chapman 1979) and Colorado (Drake and Harris 1928).

Idaho records.—Specimens have been collected on ponds, lakes, and reservoirs in protected, vegetated areas in 15 counties: Bear Lake, Benewah, Blaine, Bonner, Boundary, Canyon, Cassia, Custer, Franklin, Fremont, Kootenai, Latah, Owyhee, Payette, and Valley. Adults have been collected from March through September, nymphs from June through August.

Gerris (Gerris) comatus Drake & Hottes

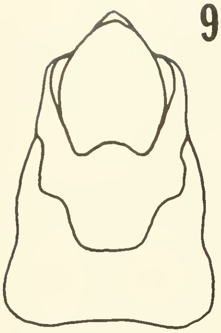
Figs. 17, 18

Gerris comatus Drake & Hottes, 1925a. Ohio J. Sci. 25: 48. Holotype, macropterous male: Estes Park, Colorado, 27 August 1924, C. J. Drake and F. C. Hottes. C. J. Drake (USNM).

Gerris comatus var. *mickeli* Drake & Hottes, 1925b. Proc. Biol. Soc. of Washington 38: 72. Holotype, brachypterous female: Rochester, Minnesota, 15 June 1922, C. E. Mickel. C. J. Drake (USNM).

Gerris comatus mickeli Drake & Hottes, Drake and Harris 1934. Annals of the Carnegie Museum 23: 193.

The females of this medium-sized species (length 7.3–9.3 mm, width 2.3–2.8 mm) are easily confused with those of *G. marginatus* Say, as both lack the anterolateral stripes on the pronotum, with the exception of the *mickeli* variety listed above. Specimens of this morph have thus far all proven to be brachypterous females. This striped morph may be the result of a recessive gene surfacing because of seasonal or environmental factors as it



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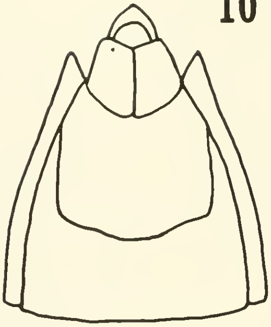

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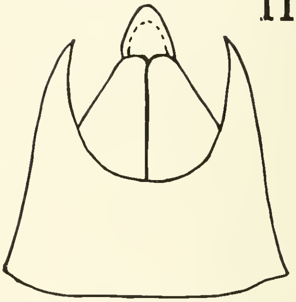

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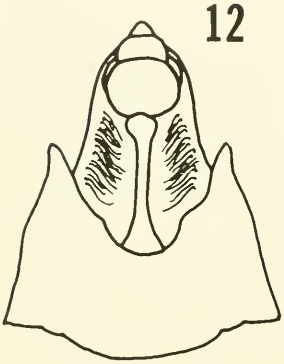

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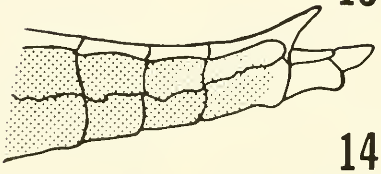

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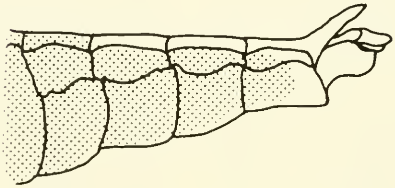

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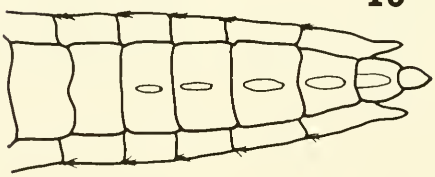

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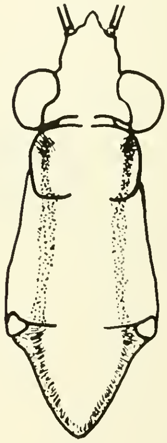

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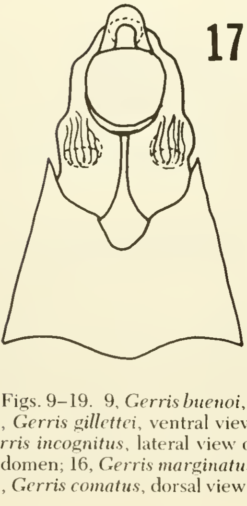
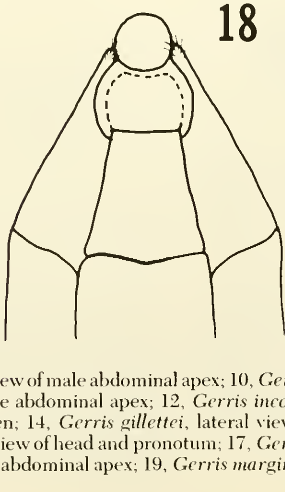
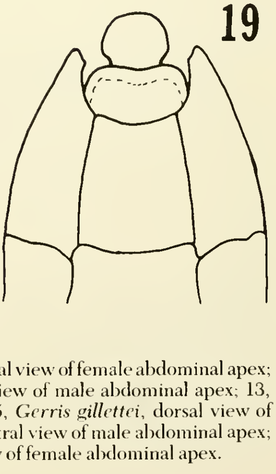


17



18



19

Figs. 9–19. 9, *Gerris buenoi*, ventral view of male abdominal apex; 10, *Gerris buenoi*, ventral view of female abdominal apex; 11, *Gerris gillettei*, ventral view of female abdominal apex; 12, *Gerris incognitus*, ventral view of male abdominal apex; 13, *gerris incognitus*, lateral view of abdomen; 14, *Gerris gillettei*, lateral view of abdomen; 15, *Gerris gillettei*, dorsal view of abdomen; 16, *Gerris marginatus*, dorsal view of head and pronotum; 17, *Gerris comatus*, ventral view of male abdominal apex; 18, *Gerris comatus*, dorsal view of female abdominal apex; 19, *Gerris marginatus*, dorsal view of female abdominal apex.

did with a similar problem in *Gerris incurvatus* Drake & Hottes (Biggam and Stock 1988). Electrophoretic analyses will probably resolve this problem. Females of normal *G. comatus* have the connexival spines short and slightly curved medially and have apical tufts of long, stiff hair; *G. marginatus* females usually have straight connexival spines with apical tufts of sparse, short hairs, similar in length to the hair on the entire spine. Male *G. comatus* have characteristic, circular tufts of long hair on the venter of abdominal segment seven on either side of the median keel. *Gerris marginatus* males lack these tufts, having only short, apressed pubescence. Another species possibly confused in some literature, *G. incurvatus* Drake & Hottes, also lacks the anterolateral, pronotal stripes but can now be easily separated from *G. comatus* and *G. marginatus* by pronotal pubescence. Dry, degreased specimens of *G. incurvatus* have only minute gold flecks, while *G. comatus* and *G. marginatus* have golden flecks interrupted by streaks or bands of reflective silvery setae. This is a new character previously unreported in literature. Apterous, brachypterous, and macropterous forms are known. The nymphs were described by Scudder and Jamieson (1972).

Geographic range.—Recorded from the Atlantic Ocean west to Montana, including New York, Iowa, South Dakota, Minnesota, Kansas, Missouri, Nebraska, Colorado, Indiana, Michigan, Pennsylvania, Ohio, Illinois, New Jersey, Maryland, and Ontario (Drake and Harris 1934), British Columbia (Scudder 1971), Quebec (Moore 1950), Alberta (Strickland 1953), Manitoba and Saskatchewan (Brooks and Kelton 1967), and Arizona, Connecticut, Florida, Oklahoma, New Hampshire, New Mexico, South Carolina, Virginia, Wisconsin, and Wyoming (Smith 1988). The subspecies *G. comatus mickeli* Drake & Hottes has been recorded from Minnesota (Drake and Hottes 1925b, as var. *mickeli*) and Oregon and Colorado (Drake and Harris 1928). The Drake & Hottes subspecies, of which only brachypterous females are known, atypically has the anterolateral, pronotal stripe. Stonedahl proposed that the *G. comatus mickeli* recorded by Drake and Hottes from Oregon was probably a misidentified *G. incurvatus*, as they found no *G. comatus* in Oregon or Washington (personal communication). Roemhild (1976) collected *G. comatus* in Montana; all specimens were taken east of the Continental Divide. Scudder (1971) listed *G. comatus* from British Columbia, Canada, which we have confirmed from specimens donated by the University of British Columbia in Vancouver. Due to their close proximity, we have included it here and in our key as a possible Idaho inhabitant.

Idaho records.—None to date.

Gerris (Gerris) gillettei Lethierry & Severin

Figs. 11, 14, 15

Limnotrechus productus Uhler, 1895. Bull. Colorado Agric. Expt. Sta. 31: 61. Holotype, female: Fort Collins, Colorado (CSU). Preoccupied in *Gerris* by *productus* Spinola, 1840.

Gerris gillettei Lethierry & Severin. 1896, Catalogue général des Hémiptéres 3: 60. New name for *productus* (Uhler).

The presence of conspicuous patches of silvery pubescence on the tergal corners of the abdomen in dry, degreased specimens will separate this species from the very similar *G. pingreensis* Drake & Hottes. Callahan (1974) stated that females of *G. gillettei* are larger on the average (10.3 mm) than females of *G. incognitus* Drake & Hottes (9.1 mm). Also, *G. gillettei* females are paler ventrally than those of *G. incognitus*. This color character was confirmed by Stonedahl and Lattin (1982). The males are easily distinguished by the presence of tufts of long hair ventrally on either side of the keel on abdominal segment seven in *G. incognitus*, and by the absence of such tufts in *G. gillettei*. *Gerris gillettei* is a medium-sized gerrid (length 8.5–11.5 mm, width 1.7–2.3 mm). The anterolateral stripe on the pronotum is present. Macropterous and apterous forms have been taken in the state, but nymphs have not yet been described.

Geographic range.—California, Colorado, Montana, Oregon, Texas, Utah, and Washington (Drake and Harris 1934), Wyoming (Kuitert 1942), Nevada (Polhemus and Chapman 1979), and British Columbia (Smith 1988). Drake and Harris (1934) recorded *G. pingreensis* from the higher altitudes of Idaho. We have not seen true *G. pingreensis* from Idaho and believe their specimens, which we have been unable to locate, are probably *G. gillettei* Lethierry & Severin.

Idaho records.—Specimens have been collected on lakes, ponds, and reservoirs in

11 counties: Ada, Blaine, Bonneville, Cassia, Custer, Fremont, Gooding, Lemhi, Oneida, Owyhee, and Twin Falls. Adults were collected from April through August, nymphs in August.

Gerris (Gerris) incognitus Drake & Hottes

Figs. 8, 12, 13

Gerris incognitus Drake & Hottes, 1925b. Proc. Biol. Soc. Wash. 38: 73. Holotype, macropterous male (erroneously stated to be female): Kaslo, British Columbia (USNM: type missing).

The longitudinal rows of long hairs lateral to the ventral keel of the male abdominal segment eight, combined with the presence of the anterolateral pronotal stripes, will easily separate this species from all other male gerrids of this size (length 6.7–11.0 mm, width 2.5–2.9 mm) found in the state. Callahan (1974) stated that females of *G. incognitus* are smaller and darker ventrally than females of *G. gillettei* Lethierry & Severin. Stonedahl and Lattin (1982) showed the light, dorsolateral, abdominal stripe extending the entire length of the abdomen (Fig. 13). Macropterous and apterous specimens are known from Idaho. Scudder and Jamieson (1972) and Spence and Scudder (1978) described the nymphs.

GEOGRAPHIC RANGE.—California, Idaho, Montana, Oregon, Washington, British Columbia, and Quebec (Drake and Harris 1934), Colorado and Wyoming (Kuitert 1942), Nevada (Polhemus and Chapman 1979), and Alberta, Manitoba, Ontario, and Saskatchewan (Smith 1988).

IDAHO RECORDS.—This species has been collected on ponds, lakes, and reservoirs in 20 counties: Bear Lake, Benewah, Blaine, Bonner, Bonneville, Boundary, Caribou, Cassia, Clearwater, Custer, Fremont, Gooding, Idaho, Latah, Lemhi, Owyhee, Shoshone, Teton, Twin Falls, and Valley. Adults were collected from March through September, nymphs from May through August.

Gerris (Gerris) incurvatus Drake & Hottes

Fig. 6

Gerris incurvatus Drake & Hottes, 1925b. Proc. Biol. Soc. Wash. 38: 72. Holotype, male: Bozeman, Montana. C. J. Drake (USNM).

The lack of pale, anterolateral stripes on the pronotum and the strongly incurved lateral spines of the female abdominal segment seven make this small species (length 7.6–10.7 mm, width 2.3–2.5 mm) easy to identify. It can be confused with *G. marginatus* Say, especially the males, as the external genitalia are similar and both species lack the anterolateral, pronotal stripe. The new character, mentioned under *G. comatus*, has been consistent in over 60 confirmed specimens of *G. marginatus* and *G. comatus;* both species have two stripes or bands of silvery pubescence interrupting the uniform covering of golden flecks found on the pronotum. This character has proven to be consistent for both sexes with midwestern and eastern specimens examined by Gary Stonedahl (New York) and Jack Lattin (Oregon) (personal communication). *Gerris incurvatus*, on the other hand, has no silvery pubescence on the pronotum, only uniform, short, golden pubescence characteristic of the subgenus *Gerris*. This character is important in separating rare and uncommon, brachypterous female forms of *G. incurvatus* that have pronotal stripes, yet have the strongly incurved connexival spines. This rare form appears to be a genetic, seasonally induced morph (Biggam and Stock 1988). Macropterous and brachypterous forms have been collected in Idaho. Scudder and Jamieson (1972) described the nymphs.

GEOGRAPHIC RANGE.—California, Idaho, Illinois, Montana, Oregon, Washington, and British Columbia (Drake and Harris 1934), Texas and Wyoming (Kuitert 1942), and Nevada (Polhemus and Chapman 1979). Although Drake and Harris (1934) listed this species from Illinois, it was not found in Indiana (Deay and Gould 1936), Missouri (Froeschner 1962), Wisconsin (Hilsenhoff 1986), or Ohio (Osborn and Drake 1915).

IDAHO RECORDS.—Specimens have been collected on ponds, lakes, and reservoirs in 23 counties: Ada, Adams, Bannock, Benewah, Blaine, Bonner, Camas, Canyon, Cassia, Franklin, Fremont, Gooding, Idaho, Kootenai, Latah, Lemhi, Lewis, Madison, Nez Perce, Owyhee, Shoshone, Twin Falls, and Washington. Adults have been collected from March through October, nymphs from May through August.

Gerris (Gerris) marginatus Say

Figs. 16, 19

Gerris marginatus Say, 1832. Descriptions of new species of heteropterous Hemiptera of North America, New Harmony, Indiana, p. 36 (Fitch reprint,

1858. Trans. New York State Agric. Soc. 17). Page 35 *in* The complete writings of Thomas Say on the entomology of North America. J. L. LeConte, ed. Vol. 1. 362 pp. Bailliere Brothers, New York. (Types destroyed.)

This medium-sized water strider (length 8.0–10.5 mm, width 2.3–2.6 mm) reportedly lacks the anterolateral stripe on the pronotum that is common in most individuals of *G. incurvatus* Drake & Hottes and *G. comatus* Drake & Hottes. However, since the latter two species include some brachypterous individuals with pronotal stripes, similar individuals of *G. marginatus* may yet be discovered. It is easily separated from *G. incurvatus* by the presence of two longitudinal bands of longer, silvery pubescence on the pronotum. This character also occurs in *G. comatus;* however, the males of *G. comatus* have circular tufts of hair ventrally on abdominal sternum eight. Males of *G. marginatus* do not have this character. The females of *G. marginatus* have the connexival spines rather straight, slightly upturned, and without strong setae at the tips. Females of *G. comatus* have the spines curving slightly inward and tipped with strong setae.

Geographic range.—Drake and Harris (1934) reported this species occurring in every state in the United States and in Canada, Mexico, and Brazil. As mentioned in the biology section, pertinent literature concerning this species is confusing, and we suspect that two or more species may have been involved in the reportings of earlier workers (Drake and Harris 1934). This may be true of the Torre-Bueno (1917b) paper on the immature stages and life history of *G. marginatus.*

Stonedahl and Lattin (1982) believed the Oregon and Washington records of Drake and Harris (1934) to be *G. incurvatus*, which apparently replaces *G. marginatus* in the West. Roemhild (1976) recorded *G. marginatus* from Montana. From his identified material, only a single specimen was recorded west of the Continental Divide. The close proximity of this species to Idaho prompts us to include it in our key as a possible inhabitant of the state.

Idaho records.—None.

Gerris (Gerris) pingreensis Drake & Hottes

Gerris pingreensis Drake & Hottes, 1925a. Ohio J. Sci. 25: 49. Holotype, macropterous male: Pingree Park, Colorado. C. J. Drake (USNM).

This species is easily confused with *G. gillettei* Lethierry & Severin. Although *G. pingreensis* and *G. gillettei* are readily separated by the conspicuous silvery patches of setae at the dorsolateral tergal apices on *G. gillettei* and their absence on *G. pingreensis*, confusion between the two species may be the result of grease or liquid preservatives that conceal these silvery hairs. *Gerris pingreensis* is similar in size to *G. buenoi* Kirkaldy (length 9.0–10.00 mm, width 2.0–2.5 mm). Macropterous and apterous forms are known for this species (Drake and Hottes 1925a). Scudder and Jamieson (1972) and Spence and Scudder (1978) described the nymphs.

Geographic range.—Streams and lakes of the higher altitudes of Montana, Colorado, Idaho, and Alberta, (Drake and Harris 1934, Strickland 1953), and British Columbia (Scudder 1971). Roemhild (1976) also records this species from Montana west of the Continental Divide. Alberta, Saskatchewan, and Manitoba (Brooks and Kelton 1967), Quebec (Moore 1950), Yukon–Northwest Territories (Scudder 1971), and Alaska (Smith 1988).

Idaho records.—The Idaho records of Drake and Harris (1934) are probably incorrect and are believed to pertain to *G. gillettei* Lethierry & Severin. We have not collected this species in Idaho, nor have we been able to locate the Drake and Harris specimens to confirm its presence in Idaho. We include it here as possibly inhabiting the higher elevations along the eastern and northern boundaries of the state.

Genus *Limnoporus* Stål

Limnoporus Stål, 1868. Ofvers. K. Vet.—Akad. Forh 25: 395. Type species: *Gerris rufoscutellatus* Latreille, 1807 monotypic.

Andersen (1975) elevated this subgenus of *Gerris* to generic status. The proportions of the antennal segments serve to separate it from the closely related *Gerris* spp. Four species are recorded from the Americas, all Nearctic. Only one species is recorded from Idaho.

Limnoporus notabilis (Drake & Hottes)

Figs. 3, 4

Gerris (Limnoporous) [sic] *notablis* [sic] Drake & Hottes, 1925a. Ohio. J. Sci. 25: 46. Holotype, macropterous male: Pingree Park, Colorado. C. J. Drake (USNM).

Gerris notabilis Drake & Hottes, 1925b. Proc. Biol. Soc. of Washington 38: 73.

This is the largest gerrid in the state (length 14.4–20.0 mm, width 2.0–2.5 mm). Its long, slender body and legs make it distinctive and easily separated from members of the genus *Gerris*. Sternum six of the males is not secondarily notched as in *Gerris* males. The very similar *L. dissortis* Drake & Harris, which occurs in the Midwest up to the Rockies, may be confused with *notabilis* because of the similar color pattern. However, *L. dissortis* is a smaller species with shorter legs than *L. notabilis*. The antennal segment ratios as described by Drake and Harris (1934) appear to be the best character for separating *L. notabilis* and *L. dissortis*, the latter being reported from British Columbia by Scudder (1977). The occurrence of hybrids between these two species in British Columbia (Spence and Maddison 1986) further complicates distribution records. Idaho *L. notabilis* have the third and fourth antennal segments subequal and each shorter than the second segment. *Limnoporus dissortis* has the second and fourth segments subequal, each longer than the third segment. Only the macropterous form is known in Idaho and the Pacific Northwest. Scudder and Jamieson (1972) described the nymphs.

GEOGRAPHIC RANGE. — California, Colorado, Idaho, Iowa, Oregon, Montana, Utah, Washington, Wyoming, and British Columbia (Drake and Harris 1934), Colorado (Drake and Harris 1935), Arizona and South Dakota (Kuitert 1942), Alberta (Brooks and Kelton 1967), and New Mexico (Smith 1988). Drake and Harris (1930) list this species as western and occurring as far east as Iowa.

IDAHO RECORDS.—This species has been collected on ponds, lakes, reservoirs, and slower moving streams and rivers in 30 counties: Ada, Adams, Bear Lake, Benewah, Blaine, Boise, Bonner, Bonneville, Boundary, Butte, Camas, Canyon, Caribou, Cassia, Clark, Custer, Elmore, Franklin, Fremont, Gem, Gooding, Idaho, Kootenai, Latah, Nez Perce, Owyhee, Payette, Shoshone, Valley, and Washington. Adults were collected from March through October, nymphs in August.

Subfamily Trepobatinae

Two of the 13 genera in this subfamily occur in North America. Only one is found in Idaho.

Genus *Metrobates* Uhler

Metrobates Uhler, 1871b. Boston Soc. Nat. Hist. 14: 108. Type species: *Metrobates hesperius* Uhler, 1871b, monotypic.

Trepobatopsis Champion, 1898. Biologia Centrali Americana, Rhynchota 2: 157.

Members of this genus have short, broad, dorsoventrally flattened abdomens. The second and third antennal segments of the male are swollen distally. The body is grey with black markings. These bugs prefer large rivers with moderate currents. Worldwide there are 14 recognized species with four subspecies. Five species occur in the United States; one species and its subspecies occur in Idaho. The genus was last revised by Anderson (1932) and Drake and Harris (1932).

Metrobates trux infuscatus Usinger

Fig. 2

Metrobates trux infuscatus Usinger, 1953. Pan-Pac. Entomol. 29: 178–179. Holotype, male: Putah Cr., Davis, California (CAS).

The short, broad, dorsoventrally flattened abdomen (length 4.0–4.6 mm) and the grey color with black markings, combined with the extremely long legs, make this unique species the most easily identified gerrid in Idaho. Apterous and rarely macropterous forms have been collected in Idaho. Nymphs of this species have not been described.

GEOGRAPHIC RANGE.—Central and northern California (Polhemus and Chapman 1979, Usinger 1953), Idaho, Washington, and Wyoming (Polhemus and Chapman 1979), Oregon (Stonedahl and Lattin 1982), and New Mexico and Arizona (Smith 1988).

Smith (1988) listed the subspecies *M. trux trux* (Torre-Bueno) from Idaho as well as Arizona, California, Colorado, Kansas, New Mexico, and Texas. Drake and Harris (1932) stated that the second antennal segment of the Texas specimens was, at least in part, yellowish brown, unlike those of Oregon and Idaho specimens. Usinger (1953) described *M. trux infuscatus* from specimens originally determined by H. B. Hungerford and L. D. Anderson as "*M. trux* Bueno," noting the darker markings of the upper surface as being more extensive than the typical form described from Colorado and recorded from Texas, Kansas, Arizona, and, apparently erroneously, Oregon and Idaho. Based on our examination of available Idaho material and Polhemus and

Chapman (1979), we suggest that *M. trux* specimens collected and identified from Oregon and Idaho prior to Usinger's description of *M. trux infuscatus* (1953) are probably the latter subspecies, despite confusion in the literature. The deletion of Idaho as a locality for *M. trux trux* (Torre-Bueno) appears advisable, leaving Arizona, (southern) California, Colorado, Kansas, New Mexico, and Texas as the more likely distribution of this subspecies. Stonedahl and Lattin (1982) contend that *M. trux infuscatus* Usinger is the only subspecies occurring in the Pacific Northwest.

IDAHO RECORDS.—This unique species has been collected on major rivers and creeks in moderate currents in four counties: Benewah, Clearwater, Latah, and Owyhee. Adults have been collected in August and September, nymphs in July and August.

ACKNOWLEDGMENTS

The authors express their gratitude to the following for their determinations, searches, loans, and other taxonomic assistance: Edwin F. Cook and Jeffrey D. Hahn, University of Minnesota; John R. Spence, University of Alberta; George R. Roemhild and Mike A. Ivie, Montana State University; John K. Bouseman, Illinois Department of Energy and Natural Resources, Champaign, Illinois; Richard C. Froeschner, U.S. National Musuem of Natural History, Smithsonian Institution; Paul Kittle, Southeast Missouri State University; Robert Lewis, Iowa State University; G. G. E. Scudder, University of British Columbia; George W. Byers, University of Kansas; Charles Baker, Boise State University; William H. Clark, College of Idaho—Caldwell; Al Allan, Boise, Idaho; Larry R. Schoenike, Island Park, Idaho; Charles E. Hornig, Redmond, Washington; Karla M. Schwartz (now Reynolds), Kuna, Idaho; Robert L. Gillespie, Montana Department of Agriculture, Helena; Daniel T. Wade, Boston, Massachusetts; John T. Polhemus, University of Colorado Museum; Gary M. Stonedahl, American Museum of Natural History—N.Y.; John D. Lattin, Oregon State University; William F. Barr, James B. Johnson, Fred W. Rabe, Frank W. Merickel, Paul E. Blom, Paul J. Johnson, and Norman A. Bowers, University of Idaho; and Cheryl L. Noble, Flagstaff, Arizona, for the illustrations.

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COMPARISON OF SAGE AND SHARP-TAILED GROUSE LEKS IN SOUTH CENTRAL WYOMING

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ABSTRACT.—Columbian Sharp-tailed Grouse (*Tympanuchus phasianellus columbianus*) and Sage Grouse (*Centrocercus urophasianus*) leks were compared in an area of sympatry in south central Wyoming. Sharp-tailed Grouse leks had more ($P < .05$) shrub cover, taller shrubs, more forb, grass, and shrub species, and less visibility than did Sage Grouse leks. Reduction in shrub cover or the diversity of herbaceous species could potentially have greater influence on the use of lek sites by Columbian Sharp-tailed Grouse than by Sage Grouse in areas of sympatry in Wyoming.

Columbian Sharp-tailed Grouse (*Tympanuchus phasianellus columbianus*) and Sage Grouse (*Centrocercus urophasianus*) occurred sympatrically over much of their historic ranges (Aldrich 1963). Viable populations of the two species now coexist only in portions of Utah, Idaho, Colorado, and Wyoming (Hart et al. 1950, Rogers 1969, Ward 1984, Oedekoven 1985). Because leks are traditional breeding areas and are the hub around which nesting occurs (Autenrieth 1986), they are important to both grouse species. Lek characteristics have been described for Sharp-tailed Grouse (Ward 1984) and Sage Grouse (Dalke et al. 1963, Rothenmaier 1979, Emmons 1980, Johnsgard 1983: 115). Characteristics of Sage Grouse and Sharp-tailed Grouse leks have not been described or compared in areas where the two species occur sympatically. Objectives of the study were to determine whether leks of the two species differed in the following characteristics: visibility, vegetal composition, vegetal structure, ecotone location, and topography.

STUDY AREA

The study area is 97 km southwest of Rawlins, Wyoming, at an elevation of 1,980–2,500 m. Soils in the area are primarily sandy loams in the Pactic Agriboroll and Haploboroll soil groups. Topography is generally flat uplands and foothills dissected by river systems. Vegetation at lower elevations is dominated by sagebrush (*Artemisia* spp.)-grass communities. Mountain shrub communities of sagebrush, mountain snowberry (*Symphoricarpos oreophileus*), and Utah serviceberry (*Amelanchier utahensis*), as well as quaking aspen (*Populus tremuloides*) stands, occur at higher elevations or at sites where snow accumulates.

METHODS

Thirteen openings each of Sharp-tailed Grouse leks and Sage Grouse leks were randomly selected for characterization. Five 20-m-long transects were positioned to radiate from the center (dominant male territory) of each lek. The direction for each transect was selected from a random numbers table. Shrub cover was measured using the line-point intercept method (Heady et al. 1959), recording shrubs hit at 0.5-m intervals. Shrub height was measured in the center of each shrub contacted. We recorded the number of shrub, grass, and forb species present at each site within a 30-m radius that encompassed the lek. A cover board was placed at the center of the lek and 10 m from the center along each transect. We counted the number of squares visible within each at a distance of 9 m and a height of 15 cm (Jones 1968) and then averaged them for statistical comparisons. Percent slope was measured with a clinometer, and elevation was taken from topographic maps. The position of the lek was classified as edge or center in the opening in which it occurred.

Shrub communities in the area were classified as sagebrush-grass, sagebrush-bitterbrush, sagebrush-snowberry, and mountain

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TABLE 1. Characteristics of random openings, Columbian Sharp-tailed and Sage Grouse leks. Means with the same letter are not different ($P < .05$).

		Sharp-tailed		Sage		Random	
Characteristics	P value	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Number		13		13		13	
Edge occurrence (%)	.233	46.15^{a}	0.52	23.98^{a}	0.44		
Elevation (m)	.643	$2,183.77^{a}$	78.90	$2,160.85^{a}$	131.75	$2,167.49^{a}$	40.09
Slope (%)	.046	$4.15^{a,b}$	3.41	2.77^{a}	1.48	6.07^{b}	3.69
Shrub cover (%)	.000	11.08^{a}	7.44	2.61^{b}	4.09	2.00^{b}	2.88
N shrub species	.000	2.54^{a}	1.05	0.85^{b}	0.69	0.79	0.98
Shrub height (cm)	.010	39.77^{a}	15.21	22.03^{b}	19.17	17.57^{b}	21.05
Number of forb species	.000	14.77^{a}	4.71	7.08^{b}	4.21	11.00^{c}	3.68
Number of grass species	.024	6.77^{a}	3.63	3.24^{b}	1.00	$4.43^{a,b}$	2.10
Visibility (%)	.000	65.23^{a}	20.69	80.24^{b}	7.54	31.69^{c}	15.53

shrub. We characterized vegetation at randomly located points within each habitat with the same methods used to measure variables at leks, except that we used four transects instead of five to reduce sampling effort. Points were selected using a random numbers table to determine bearing, starting location (1/4 of 1/4 section), and habitat. The bearing was followed until the habitat was encountered; the plot center was then placed a minimum of 25 m from the ecotone. Vegetation sampling was conducted between mid-April and early June 1986 to minimize the influence of seasonal shifts in plant species composition.

T-tests (Ott 1984, Wilkinson 1986) were used to determine edge occurrence, while analysis of variance (Ott 1984, Wilkinson 1986) was used to examine other characteristics. Statistical comparisons with differences of $P < .05$ were considered significant. Newman-Kuels post hoc tests were used to determine differences between groups when analyses of variance results were significant (Wilkinson 1986).

RESULTS

Columbian Sharp-tailed Grouse leks had greater shrub cover, taller shrubs, and greater numbers of shrub, forb, and grass species ($P < .05$) than did Sage Grouse leks (Table 1). Sharp-tailed Grouse leks were typically on steeper slopes, at higher elevations, and at the edge of openings more often than were Sage Grouse leks ($P < .05$). Visibility was greatest on Sage Grouse leks and least in random openings. Sixty randomly located shrub plots within 3 km of leks averaged 42.1% shrub cover, 71.8 cm shrub height, 11.8 forb species, 6.6 grass species, and 4% visibility. Shrub cover and shrub height were greater, while visibility was less ($P < .05$), at shrub plots compared to leks.

DISCUSSION

Visibility on leks is important for ritualized displays of male grouse (Wiley 1978) and for attracting female grouse to the lek (Rothenmaier 1979, Ward 1984). Leks of Sage and Sharp-tailed Grouse in Wyoming had greater visibility than did random openings. Our data indicated that the visibility on the Sage Grouse leks was near the optimum (70–80%) reported by Ward (1984), while visibility on Sharp-tailed Grouse leks was slightly above optimum for that species. Kobriger (1965) noted that Prairie Grouse can considerably reduce herbaceous vegetation on a lek by trampling. We noted a similar effect on forbs and grasses at the leks we observed, suggesting that the primary difference between Sage and Sharp-tailed Grouse leks was in the amount of shrub cover present.

Cover is important in predator detection and avoidance. Ward (1984) found that Columbian Sharp-tailed Grouse used the more open areas of their territories on the lek when females were present, but stayed in areas with more cover when females were absent. Jones (1968) reported that Sharp-tailed Grouse moved behind cover when they detected predators. Marks and Marks (1987a) believed that Sharp-tailed Grouse were vulnerable to avian predation while attending leks, and Hartzler (1974) reported that predation influenced the time of activity of Sage Grouse on leks. Dead Sharp-tailed Grouse found by

Ward (1984) were all in areas of the lek with 70–80% visibility. We found remains of five Sage and eight Sharp-tailed Grouse on leks. Four of the Sage Grouse and all of the Sharp-tailed Grouse carcasses were found in open areas within the lek.

The amount of cover (herbaceous and shrubby) on a lek appears to represent a tradeoff between high visibility desirable for breeding and displaying and lower visibility that enhances security. We frequently observed male Sharp-tailed Grouse at six leks cooing and gobbling while perched on shrubs. They used these shrubby sites even though open areas were available within 200 m of each lek. Rothenmaier (1979) found that Sage Grouse leks on large playas in eastern Wyoming were located near the sagebrush edge rather than the center openings. Ward (1984) similarly found that Sharp-tailed Grouse avoided open areas on leks, reporting that areas with 95–100% visibility were used significantly less than areas with lower visibility. Shrub cover values at randomly located plots within 3 km of the leks we observed were similar to those found by other researchers (Wallestad and Schladweiler 1974, Rothenmaier 1979, Oedekoven 1985).

Shrubs may contribute to grouse security also by providing vantage points at leks. Moyles and Boag (1981) reported that juvenile male Sharp-tailed Grouse of the plains subspecies (*T. p. jamesii*) used elevated vantage points to observe displaying adults in the fall prior to establishing territories on the lek. They believed that the elevated positions gave the juvenile males immunity from attack by territorial males.

Columbian Sharp-tailed Grouse may also select lek sites on the basis of food availability. Sharp-tailed Grouse displayed at leks in the fall (late August through September). Marks and Marks (1987b) also reported male Sharp-tailed Grouse displaying at leks in western Idaho in the fall. Moyles and Boag (1981) suggested that most of the recruitment (68%) of young (six months of age) male Plains Sharp-tailed Grouse to a lek occurred during the fall. In south central Wyoming some plant species, such as needle grass (*Stipa* spp.), are senescent, while others, such as bluegrass (*Poa* spp.) and dandelion (*Taraxacum officinale*), are still somewhat succulent by fall. These species were present at most Sharp-tailed Grouse leks and are fall foods of Sharp-tails (Jones 1966). Blus (1967) reported one case of Plains Sharp-tailed Grouse shifting their lek in response to available forage in the spring, and Sisson (1976) believed that there was a relationship between lek location and winter foraging areas. Sage Grouse, on the other hand, do not typically display at leks in the fall and switch to a diet composed predominantly of sagebrush at this time (Wallestad 1975).

Several authors have reported that Sage Grouse may change the location of the lek following habitat disturbance (shrub removal) (Dalke et al. 1963, Connelly et al. 1981). Sage Grouse switched to disturbed sites, but only when there were relatively few openings in the surrounding habitat (Connelly et al. 1981). Sexton and Gillespie (1979) reported that Plains Sharp-tailed Grouse moved to a burned area, but the burn included historic lek site. Short-term benefits of fire include more nutritious vegetation (Barbour et al. 1980: 381, Wright and Bailey 1980) and a reduction in litter (Sexton and Gillespie 1979, Wright and Bailey 1980), which makes new growth more visible.

Our data suggest that while Sage Grouse leks may be enhanced by cover-reducing treatments, such treatments would be less beneficial on Columbian Sharp-tailed Grouse leks because Sharp-tailed Grouse use leks with more shrub cover than do Sage Grouse. Boyce (1981) suggested that areas with a high degree of patchiness provide better quality grouse habitat than do areas with uniform vegetation. Large treatments would reduce habitat and thus be detrimental to both species (Martin 1970, Klebenow 1972, Oedekoven 1985). While the lek is an important component of grouse habitat, other habitat features that provide nesting, brooding, and wintering requirements also need to be considered in management of these species.

ACKNOWLEDGMENTS

We appreciate the help of D. Moody of the Wyoming Game and Fish Department for assistance in identifying Sage Grouse leks and S. Gallagher for assisting with vegetation sampling. M. S. Boyce, W. R. Eddleman, and W. B. Sidle provided comments on the manuscript. This study was conducted under the auspices of the Wyoming Cooperative

Fishery and Wildlife Research Unit, U.S. Fish and Wildlife Service, University of Wyoming and the Wyoming Game and Fish Department. Funding for the project was provided by the Bureau of Land Management, Rawlins District.

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NOTES ON HELLS CANYON BIRDS

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ABSTRACT.—An annotated list of 108 bird species is reported from several spring and two summer visits, as well as one fall and one winter visit, into Hells Canyon on the Idaho-Oregon border. This is the first report on the avifauna of one of the deepest gorges on earth.

With a maximum depth of 2,400 m (Ashworth 1977), Hells Canyon is one of the deepest gorges on earth. The Snake River runs through the canyon and forms part of the border between Idaho and Oregon. Hells Canyon, lying on a north-south axis, is narrow, varying from about 8 to 16 km from rim to rim. It is characterized by basalt cliffs, outcrops, and scree fields interspersed with grassy benches and steep slopes. Small streams cascade down the canyon walls every few or several miles. The canyon bottom varies from about 400 to 500 m in elevation, approximately the elevation of Lewiston, which is the lowest point in Idaho (Burleigh 1972). Summers are hot and dry, and winters are cool and wet, although snow only rarely stays on the canyon bottom (J. Zanelli, personal communication).

A party from the Lewis and Clark Expedition briefly explored the lower regions of Hells Canyon at the beginning of the nineteenth century, and cattle ranching has occurred there for over a century (Ashworth 1977), but the canyon has been little explored by biologists, particularly Idaho ornithologists. The two books on Idaho birdlife (Larrison et al. 1967, Burleigh 1972) are almost devoid of records from Hells Canyon. A recent review of the ornithological literature of Idaho (J. M. Scott, M.S.) found no references for Hells Canyon. The nearest Idaho references are Burleigh's numerous records from Lewiston, near the north end of Hells Canyon, and an annotated list from the Weiser Valley south of Hells Canyon by Newhouse (1960). The nearest Oregon reference to Hells Canyon known to me is the general annotated list for Union and Wallowa counties by the Grande Rounde Bird Club (undated, probably 1980). To fill in this gap in knowledge of Idaho bird distribution, I report in this paper observations of birds made during several trips into this canyon by myself and others.

The lack of bird records from Hells Canyon is probably due to the canyon's ruggedness and isolation. On the Idaho side public access is limited to a paved road along the 50 km of reservoirs behind Oxbow and Hells Canyon dams on the upper or south end of the canyon. The Snake River below the dam is free flowing the remaining 125 km of the canyon, and much is designated a Wild and Scenic River. There is a rough dirt road at Pittsburg Landing, 52 km below Hells Canyon Dam, and there are a few hiking trails down to the river through the Seven Devils Mountains.

The ground layer of vegetation consists of bunch grasses and herbs, of which 24 endemic species were recorded as in the canyon (Ashworth 1977). Prickly-pear cactus (*Opuntia polyacantha*) is commonly found, especially in the northern half. Shrubs are patchy and usually in more mesic locations. Common deciduous tree and shrub species are poison oak (*Toxifolia radicans*), currants (*Ribes* spp.), western serviceberry (*Amelanchier alnifolia*), mountain mahogany (*Cercocarpus ledifolius*), hawthorne (*Crataegus douglasii*), syringa (*Philadelphus lewisii*), red-osier dogwood (*Cornus stolonifera*), chokecherry (*Prunus virginiana*), alder (*Alnus rhombifolia*), willow (*Salix* spp.), and cottonwood (*Populus trichocarpa*) (Bingham and Henderson 1978). The latter four species are confined mostly to riparian zones along small streams. There is practically no riparian brush along the main river, probably because of the strong and erratic fluctuations in water levels and the characteristically steep and rocky shoreline. I found no big sagebrush (*Artemisia tridentata*) the entire length of the canyon, and the only shrub typical of xeric sites in the cold deserts of Idaho and Oregon is rabbitbrush (*Chrysothamnus* sp.), which occurs only in the last 8 km of the north end of the canyon. The only common tree away from riparian zones at the bottom of the canyon is hackberry (*Celtis reticulata*), which is common the entire length of the canyon. There are sporadic small clumps of ponderosa pine (*Pinus ponderosa*) as well as lone individuals near the river, and groves are found down to the canyon bottom along at least Granite and Kirkwood creeks.

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The higher sections of Hells Canyon are often timbered by ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*). There are also grassy hillsides and meadows at these higher elevations.

Study Areas and Methods

Observations of birds along the reservoirs above Hells Canyon Dam have been limited to a few days in spring when I was driving to the boat launch just below the dam. I took hiking trips downstream from Hells Canyon Dam on 21–25 March and 9–12 December 1979, 8–10 April 1980, 18–22 March 1981, and 14–17 March 1984. I also received records from a 10–15 May 1987 hike in that area by Andy and Dr. S. C. Taylor. The farthest downstream extension of these hikes was 11 km to Granite Creek. Another hike was taken from Pittsburg Landing, 24 km upstream to Sheep Creek, 13–17 March 1983. A day hike from Pittsburg Landing upstream 6 km occurred 22 May 1986. I took a raft float trip from Hells Canyon Dam downstream 126 km to Hellar Bar 22–27 August 1987. I also received records by Peter Warshall, who took a similar float trip on 18–22 July 1986. A hike from the rim of the canyon 11 km down to the mouth of Sheep Creek along the Stormy Point Trail was taken 27–29 September 1988.

Birds were recorded opportunistically as they were encountered. Most mornings I took walks along the Snake River's bank or up creeks entering the river. I used 7 × 35-mm binoculars to help identify birds. Most observations were made within 1,000 m of the canyon floor, and comparatively little time was spent in the coniferous forests.

Species Accounts

Pied-billed Grebe (*Podilymbus podiceps*). This species was recorded on the July 1986 float trip by Peter Warshall.

Great Blue Heron (*Ardea herodias*). I saw one specimen while I was driving along one of the reservoirs on 18 March 1981. Records below Hells Canyon Dam are all from summer, with six and nine birds recorded respectively on the July 1986 and August 1987 float trips. The birds I observed fed alone in shallow water or were flying overhead and were found from Bernard Creek downstream to Hellar Bar.

Swan (*Cygnus* sp.). Three swans, probably Tundra Swans (*C. columbianus*) but possibly Trumpeter Swans (*C. buccinator*), were flying north about 150 m above the river near Brush Creek on 25 March 1979. Swans were heard overhead the evening of 18 March 1981 at Granite Creek.

Snow Goose (*Chen caerulescens*). About 35 white-phased geese were flying north 100 m above the Snake River near Brush Creek on 25 March 1979.

Canada Goose (*Branta canadensis*). An individual and a pair were flying over the Snake River near Granite Creek on 11 December 1979 and 22 March 1981, respectively. Small flocks were on the river or grazing in a small flooded pasture from Pittsburg Landing to Sheep Creek in March 1983 and May 1986. More than 20 were found molting during the July 1986 float trip.

Mallard (*Anas platyrhychos*). A bird was about 2 km upstream from Sheep Creek on 17 March 1983, and a female was seen on the July 1986 float trip.

Northern Pintail (*A. acuta*). A pair was flying high over the Snake River near Granite Creek on 19 March 1981.

Northern Shoveler (*A. clypeata*). Fourteen were flying south above the Snake River on 26 August 1987.

American Wigeon (*A. americana*). Four were on a quiet eddy of the Snake River near Granite Creek on 14 March 1984.

Common Goldeneye (*Bucephala clangula*). About 12 were congregated with Barrow's Goldeneyes on the Snake River near Brush Creek on 8–10 December 1979.

Barrow's Goldeneye (*B. islandica*). Between 9 and 60 individuals were found between Hells Canyon Dam and Granite Creek on the four early spring trips and one winter trip into this area. The birds were usually in flocks on the Snake River, where they dived into swift but smooth water. Birds were molting into breeding plumage in March.

Common Merganser (*Mergus merganser*). Up to nine birds were found on all early spring trips and the winter trip into Granite Creek. A single bird was seen 13–17 March 1983 between Pittsburg Landing and Sheep Creek. A flock with one bird in male plumage and five in female plumage was on Hells Canyon Reservoir on 8 April 1980. A total of 23 were seen on the August 1987 float trip.

Turkey Vulture (*Cathartes aura*). One was flying above Oxbow Dam on 8 April 1980.

Osprey (*Pandion haliaetus*). One was observed on the July 1986 float trip.

Bald Eagle (*Haliaeetus leucocephalus*). Along the reservoirs, five adults and an immature were found on 21 March 1979, two adults and an immature on 18 March 1981, and two on 14 March 1984. Several were also seen along the reservoirs during winter in the late 1970s by John S. Taylor. Below Hells Canyon Dam one was seen 13 December 1979 at Brush Creek, and two adults were seen between Brush Creek and Granite Creek on 17 March 1984. A pair nested in a big, lone ponderosa pine at the mouth of Two Creeks earlier in the twentieth century (Carrey et al. 1979: 166).

Cooper's Hawk (*Accipiter cooperii*). One bird was being attacked by an American Kestrel in the Bernard Creek area on 23 August 1987. Another individual was soaring along the rim of the canyon at the head of Stormy Point Trail on 29 September 1988.

Goshawk (*A. gentilis*). One bird was flying over conifer forest along Granite Creek on 15 March 1984.

Red-tailed Hawk (*Buteo jamaicensis*). One unaged bird was at Oxbow Dam on 8 April 1980. An adult was calling between Pittsburg Landing and Sheep Creek on 13 March 1983. Two or three pairs were observed during the July 1986 float trip. An adult was soaring along the canyon rim near the head of Stormy Point Trail on 29 September 1988.

Golden Eagle (*Aquila chrysaetos*). This eagle was recorded on nearly every trip in all seasons and was found the length of the canyon. Most sightings were of lone or paired adults, with a high daily count of nine on 13 March 1983 between Pittsburg Landing and Sheep Creek. Courtship behavior was observed several times in spring. On 29 September 1988 an immature was flushed from a recently killed mule deer (*Odocoileus hemionus*) on upper Sheep Creek.

American Kestrel (*Falco sparverius*). The only spring record is of one bird at Granite Creek in mid-May 1986. On the August 1987 float trip I saw a total of 11 birds from Bernard Creek downstream to Hellar Bar. One kestrel was seen about 1 km downstream from Rush Creek on 28 September 1988.

Ruffed Grouse (*Bonasa umbellus*). One to three individuals were recorded in March and December 1979 and in April 1980 at Granite Creek, and a total of four birds were found along Sheep Creek 27–29 September 1980. Birds have been found in riparian brush or in conifer forest, and drumming birds were heard in April and September.

Blue Grouse (*Dendragapus obscurus*). Two groups totaling eight birds were flushed from riparian brush mixed with conifer forest on upper Sheep Creek on 29 September 1988.

Chukar (*Alectoris chukar*). I found this introduced species to be a common resident the entire length of the canyon. It could be heard throughout the year calling from rocky, open areas. Coveys were often observed coming down to the river to drink during August 1987.

Gray Partridge (*Perdix perdix*). A covey was along Hells Canyon Reservoir on 21 March 1979.

Killdeer (*Chardrius vociferus*). Two or three birds were in a flooded pasture at Pittsburg Landing on 13 March 1983. Another one was observed at Dry Gulch, Oregon, on 23 August 1987.

Spotted Sandpiper (*Actitis macularia*). At least five were recorded on the July 1986 float trip, some of which were protecting nests. A total of 30 birds were found alone or in pairs in August 1987.

Western Sandpiper (*Calidris mauri*). About 15 were flying low and fast downstream (north) about 5 km downstream from Pittsburg Landing on 24 August 1987.

Ring-billed Gull (*Larus delawarensis*). An adult was resting on Hells Canyon Reservoir about 2 km above the dam on 22 August 1987. Another was sighted just below Hells Canyon Dam on 22 March 1981.

California Gull (*L. californicus*). A single bird was seen near the spillway of Oxbow Dam on 8 April 1980. Immatures and adults were found on the July 1986 float trip.

Rock Dove (*Columba livia*). This species was recorded on the July 1986 float trip.

Mourning Dove (*Zenaida macroura*). This dove was recorded on the July 1986 float trip. Two were flushed from the road along Hells Canyon Reservoir on 22 August 1987, and about 20 were also seen on the August 1987 float trip.

Western Screech Owl (*Otus kennicottii*). This species was heard calling from hackberry groves at Granite Creek on 21–22 March 1981 and 14–16 March 1984. Others were calling near Brush Creek on 17 March 1984 and at Pittsburg Landing on 13 March 1983.

Great Horned Owl (*Bubo virginianus*). Birds were heard hooting just upstream from Hells Canyon Dam on 18 March 1981, at Kirby Creek on 17 March 1983, and Dry Gulch below Granite Creek on 22 August 1987. Young were heard food-begging at Dug Creek 23 August 1987. One was hooting at the mouth of Sheep Creek on 27 September 1988.

Long-eared Owl (*Asio otus*). One owl was heard calling from a hackberry grove at Dry Gulch on the Oregon side on 24 August 1987, and another was at Cottonwood Creek two days later.

Common Nighthawk (*Chordeiles minor*). About 10 were found on the July 1986 float trip, and 7 were found between Dry Gulch on the Oregon side and about 10 km below Pittsburg Landing on the August 1987 float trip.

White-throated Swift (*Aeronautes saxatalis*). One was flying north about 1,000 m above the canyon bottom about 2 km downstream from Granite Creek on 15 March 1984. They were also recorded on the July 1986 float trip.

Vaux's Swift (*Chaetura vauxi*). About 30 of these swifts were mixed with 40 Cliff Swallows flying over the Snake River near Bernard Creek on 23 August 1987. Twelve more were at the old Len Jordan Ranch the next day.

Belted Kingfisher (*Ceryle alcyon*). One bird was along the Snake River near Granite Creek on 9 April 1980. More than 5 pairs were seen on the July 1986 float trip, and on the August 1987 float trip I recorded 15 birds from Temperance Creek to near Hellar Bar, with all but 2 birds seen below Pittsburg Landing. One was at the mouth of Sheep Creek on 27–28 September 1988.

Lewis' Woodpecker (*Melanerpes lewis*). About six birds were seen during the July 1986 float trip, and six were seen in the Granite Creek area 10–15 May 1987.

Downy Woodpecker (*Picoides pubescens*). A male was drumming on an old stump near Hibb's Cabin on Granite Creek on 10 April 1980. On 29 September 1988 one of undetermined sex was in a mixed-species flock, including Red-breasted Nuthatches, Mountain Chickadees, and Black-capped Chickadees, in riparian brush along Sheep Creek about 6 km above the Snake River.

Hairy Woodpecker (*P. villosus*). One female was seen in riparian brush along Granite Creek in March 1979 and 1981.

Common Flicker (*Colaptes auratus*). This is a fairly common resident I found the length of the canyon in riparian brush, conifer forest, grassy slopes, and a small park on Hells Canyon Reservoir. A pair at Granite Creek on 21 March 1981 included one bird with yellow flight feathers with a slight orange tinge, but with a red "mustache."

Pileated Woodpecker (*Dryocopus pileatus*). The characteristic, large, rectangular and oval holes this species leaves in wood (National Geographic 1983) were found in conifer forest along upper Sheep Creek on 27 September 1988.

Western Wood-pewee (*Contopus sordidulus*). Two pewees were seen at different locations a few km above Pittsburg Landing on 24 August 1987.

Say's Phoebe (*Sayornis saya*). I found this phoebe to be fairly common in spring and summer in the canyon. A total of 8 birds were found on the spring hikes into Granite Creek, and 15 birds were observed on the two spring hikes upstream from Pittsburg Landing. They were recorded on the July 1986 float trip. Phoebes were usually found in open, rocky or brushy habitat and were actively singing in March.

Western Kingbird (*Tyrannus verticalis*). Six of these kingbirds were in a shelter belt of trees near the ranch of Pittsburg Landing, and another was about 2 km upstream in some willows on 22 May 1986. Adults with fledglings were found on the July 1986 float trip.

Eastern Kingbird (*T. tyrannus*). This species was found on the July 1986 float trip, and on the August 1987 float trip six birds were found from about 5 km below the old Len Jordan Ranch to near Hellar Bar.

Horned Lark (*Eremophila alpestris*). This species was recorded on the July 1986 float trip.

Tree Swallow (*Tachycineta bicolor*). Six birds were flying over the Snake River near Suicide Point on 17 March 1983.

Violet-green Swallow (*T. thalassina*). This swallow was commonly seen 21–25 March 1979 from Hells Canyon Dam to Granite Creek. A few of these swallows were at Oxbow Dam, and 20 more were at Brush Creek on 8 April 1980. About 5 were seen 3 km above Pittsburg Landing on 22 May 1986, and they were also observed on the July 1986 float trip.

Northern Rough-winged Swallow (*Stelgidopteryx serripennis*). Several were flying over the Snake River with Bank Swallows at Pittsburg Landing on 22 May 1986, and one was observed gathering grass stems there. A few were seen on 24 August 1987 from Dry Gulch on the Oregon side to Tyron Creek.

Bank Swallow (*Riparia riparia*). Some were mixed in with Northern Rough-winged Swallows at Pittsburg Landing on 22 May 1986. They were also found on the July 1986 float trip.

Cliff Swallow (*Hirundo pyrrhonota*). One swallow was flying around Oxbow Dam on 8 April 1980. About 12 birds were at Pittsburg Landing on 22 May 1986. Several individuals were seen between Tyron Creek and Robinson Gulch on 25 August 1987, and a flock of 40 was near Wild Sheep Rapids the previous day.

Barn Swallow (*H. rustica*). A few birds were over the Snake River about 3–6 km above Pittsburg Landing on 22 May 1986. They were found on the July 1986 float trip, and three were at the boat ramp below Hells Canyon Dam on 22 August 1987.

Steller's Jay (*Cyanocitta stelleri*). One to four birds have been recorded from conifer forest along Granite Creek on 11–12 December 1979, 9 April 1980, and 14 March 1984. Groups of two and three birds were seen in conifer forest near Sheep Creek on the upper part of Stormy Point Trail on 27 September 1988.

Clark's Nutcracker (*Nucifraga columbiana*). A pair was in conifer forest at the saddle above Pittsburg Landing on 22 May 1986. In the conifer forest along the upper portion of Stormy Point Trail a total of 18 and 23 birds were seen respectively on 27 and 29 September 1988, and some of these birds were seen prying into ponderosa pine cones.

Black-billed Magpie (*Pica pica*). I have found this species to be a common resident throughout the canyon alone or in small flocks. Magpies were recorded on every trip into the canyon. They were found in all terrestrial habitats and at all elevations. Nests were found in hackberry tree groves.

Common Crow (*Corvus brachyrhynchos*). Crows were found on all the spring, summer, and fall trips I took into the canyon except for the 22 May 1986 day hike 6 km upstream from Pittsburg Landing. Birds were found from the reservoirs downstream to Robinson Gulch. They were seen alone or in flocks of up to 25 birds. Crows were observed in a variety of habitats at lower elevations in the canyon and were frequently associated with ranches or livestock.

Common Raven (*C. corax*). One raven was seen along the reservoirs on 21 March 1979, and an individual was reported from the July 1986 float trip. Two ravens were at the top of Stormy Point Trail on 29 September 1988 in conifer forest. Larrison et al. (1967) stated that a few birds may occur in the canyon.

Black-capped Chickadee (*Parus atricapillus*). This chickadee was recorded on every trip into the canyon. Although most commonly found in hackberry groves, it was also seen in riparian brush and ponderosa pine forest. It was often associated with Golden-crowned Kinglets and sometimes with Brown Creepers, Red-breasted Nuthatches, and Mountain Chickadees.

Mountain Chickadee (*P. gambeli*). Two of these chickadees were found in conifer forest up Granite Creek on both 12 December 1979 and 15 March 1984. A total of 11 were found in conifer forest or riparian brush along Sheep Creek on 29 September 1988. This species was sometimes associated with Golden-crowned Kinglets, Brown Creepers, Black-capped Chickadees, and Red-breasted Nuthatches.

Red-breasted Nuthatch (*Sitta canadensis*). One bird was observed in a mixed conifer forest up Granite Creek on 20 March 1981. Two were in similar forest at the saddle above

Pittsburg Landing on both 14 March 1983 and 22 May 1986. An estimated 39 Red-breasted Nuthatches were counted in the conifer forest along upper Sheep Creek 27–29 September 1988. Three were in a mixed-species flock that included a Downy Woodpecker and Mountain and Black-capped Chickadees.

Pygmy Nuthatch (*S. pygmaea*). Two birds were seen near Brush Creek in open ponderosa pine forest on 12 December 1979, and one was heard a day earlier in the Granite Creek area.

Brown Creeper (*Certhia americana*). One to four birds were in a conifer forest along Brush Creek 10–12 December 1979. One bird was on an old fruit tree at Hibb's Cabin along Granite Creek on 9 April 1980, and another was near there in a lone ponderosa pine by the Snake River on 18 March 1981.

Rock Wren (*Salpinctes obsoletus*). I found this wren to be a fairly common spring and summer bird in the canyon, except apparently in the rugged country around Granite Creek. About 12 birds were recorded on the August 1987 float trip from Suicide Point downstream to Hellar Bar.

Canyon Wren (*Catherpes mexicanus*). This wren is a common resident found the length of the canyon, and I recorded it every trip into the canyon in all seasons. Up to 7 per day have been observed at Granite Creek in spring, and 15 were heard singing 13–15 March 1983 from Sheep Creek to Pittsburg Landing. A total of 65 were recorded on the August 1987 float trip. Larrison et al. (1967) stated that this wren was common in the canyon. I observed them in brushy scree fields, around big boulders, and on rock walls.

House Wren (*Troglodytes aedon*). Two different birds were heard 2–4 km above Pittsburg Landing on 22 May 1986.

Winter Wren (*T. troglodytes*). One to two were found in riparian brush along Granite Creek on 10 April 1980, 19–22 March 1981, and 15 March 1984. One was singing along Sheep Creek about 1 km above the Snake River on 16 March 1983.

American Dipper (*Cinclus mexicanus*). Dippers were found throughout the year along numerous creeks in the canyon. They were consistently heard singing in March and April, and a pair was seen copulating along Granite Creek in mid-May 1987. In December 1979 several were seen along the Snake River between Hells Canyon Dam and Granite Creek. In spring and summer they were associated only with the creeks, except for one observed flying up the spillway of Oxbow Dam on 8 April 1980. Several times on 28 September 1988 I saw a dipper fly distances along the Snake River, then back to the mouth of Sheep Creek.

Golden-crowned Kinglet (*Regulus satrapa*). This kinglet was found at low elevations in both deciduous and conifer forests at Granite Creek on 10–12 December 1979 and in mid-March 1981 and 1984. One I recorded at Granite Creek on 9 April 1980 was high above the canyon bottom in conifer forest. Two of these kinglets were along Sheep Creek in a conifer forest on 27 September 1988, and two more were in the same area in riparian forest on 29 September 1988. These kinglets were sometimes associated with both chickadee species, Ruby-crowned Kinglets, and Brown Creepers.

Ruby-crowned Kinglet (*R. calendula*). This kinglet was seen several times in riparian brush along Granite Creek 19–22 March 1981, sometimes in association with Golden-crowned Kinglets. Along Sheep Creek on 27 September 1988 one Ruby-crowned Kinglet was in a conifer forest, and two were in riparian forest.

Mountain Bluebird (*Sialia currucoides*). Two of these bluebirds were on a grassy slope about 1,500 m above the canyon bottom near Granite Creek on 16 March 1984. Another was in a small flock of American Robins in a high meadow near the saddle above Pittsburg Landing on 13 March 1983. Larrison et al. (1967) stated that a few were found in the canyon.

Western Bluebird (*S. mexicana*). Eight of these bluebirds were perched on top of a Douglas-fir tree in open conifer forest on the rim of the canyon near the head of Stormy Point Trail on 29 September 1988.

Townsend's Solitaire (*Myadestes townsendi*). One bird was heard along Granite Creek on 15 March 1984.

Hermit Thrush (*Catharus guttatus*). This species breeds in the conifer forests of the canyon (Larrison et al. 1967).

American Robin (*Turdus migratorius*). Robins were found during all spring and summer trips, and along Sheep Creek in the fall. They were found the length of the canyon, usually in hackberry trees, riparian brush, or meadows. Migratory flocks were common in March; I saw 12 at Granite Creek on 19 March 1981 and over 100 while I was hiking from Sheep Creek to Kirk Creek on 17 March 1983.

Sage Thrasher (*Orescoptes montanus*). One was near a ranch at Pittsburg Landing on 22 May 1986.

Water Pipit (*Anthus spinoletta*). A flock of nine pipits was on an open, grassy bluff along the rim of the canyon near Stormy Point Trail on 27 September 1988.

Cedar Waxwing (*Bombycilla cedrorum*). Two small flocks were seen on a 6-km hike along the Snake River upstream from Pittsburg Landing on 22 May 1986. They were also found on the July 1986 float trip. I found individuals and small flocks at about a dozen different locations on the August 1987 float trip from Dry Gulch on the Oregon side downstream to Hellar Bar, with the largest group of 12 recorded at the old Len Jordan Ranch.

Shrike (*Lanius* sp.). One shrike was in brush along Hells Canyon Reservoir about 1 km upstream from Hells Canyon Dam on 18 March 1981.

European Starling (*Sturnus vulgaris*). A flock was at a cattle feedlot along one of the reservoirs on 22 March 1981. One starling was at Sheep Creek on 16 March 1981. Two birds were on the Idaho side of the canyon opposite Dry Gulch in Oregon on 23 August 1988, and about 5–10 were at a ranch near Temperance Creek the following day.

Warbling Vireo (*Vireo gilvus*). This species was recorded on the July 1986 float trip.

Red-eyed Vireo (*Vireo olivaceus*). This species was recorded on the July 1986 float trip.

Orange-crowned Warbler (*Vermivora celata*). One warbler was along a small stream about 3 km above Pittsburg Landing on 22 May 1986. This species was recorded on the July 1986 float trip. Two of these warblers were at the mouth of Bernard Creek on 23 August 1987, and two more were at Temperance Creek the next day.

Yellow Warbler (*Dendroica petechia*). Birds with fledgling young were seen on the July 1986 float trip. Two of these warblers were in some brush on a bench about 4 km upstream from Pittsburg Landing on 22 May 1986, and one was at Tyron Creek on 25 August 1987.

Yellow-rumped Warbler (*D. coronata*). One warbler was along Oxbow Reservoir on 18 March 1981, and two were at Granite Creek the next day. Three different sightings of this warbler were made in a 6-km walk upstream from Pittsburg Landing on 22 May 1986. One was at Lower Dry Gulch on the Idaho side and another at Dry Gulch on the Oregon side on 23 August 1987. A total of 10 birds were seen 27–29 September 1988 along Sheep Creek, most of which were associated with hackberry trees.

MacGillivary's Warbler (*Oporornis tolimei*). This species was recorded on the July 1986 float trip.

Wilson's Warbler (*Wilsonia pusilla*). One individual was along a small creek about 3 km upstream from Pittsburg Landing on 22 May 1986.

Western Tanager (*Piranga ludoviciana*). Two tanagers were seen at Granite Creek in mid-May 1987. Another tanager was at Pittsburg Landing on 22 May 1986. Adults with fledgling young were found on the July 1986 float trip, and one tanager was seen at the old Len Jordan Ranch on 24 August 1987.

Lazuli Bunting (*Passerina amoena*). This was a very common bird in May at both Granite Creek and Pittsburg Landing. Roughly 30 birds, mostly singing males, were found on a 6-km hike upstream from Pittsburg Landing on 22 May 1986. This species was the most common singing bird on the July 1986 float trip, but only a few female and immature birds were seen during the August 1987 float trip.

Rufous-sided Towhee (*Pipilio erythrophthalmus*). Single individuals were singing along Granite Creek on 10 April 1980 and 20 March 1981. One bird was seen between Pittsburg Landing and Sheep Creek on 14 March 1983, and three birds were singing from different patches of shrubs during a 6-km hike upstream from Pittsburg Landing on 22 May 1986. Three individuals were in some brush near the top of Stormy Point Trail on 27 September 1988.

Chipping Sparrow (*Spizella passerina*). Two individuals were in ponderosa pine forest at the saddle above Pittsburg Landing on 22 May 1986. One bird was in a hackberry tree 1 km below Rush Creek on 28 September 1988.

Fox Sparrow (*Passerella iliaca*). One gray-headed morph was singing near Granite Creek from a bush on a bench on 22 May 1981.

Song Sparrow (*Melospiza melodia*). I found this species to be a fairly common resident the length of the canyon, and it was recorded on every trip into the canyon. These sparrows were usually found in riparian vegetation along nearly every stream I explored in the canyon. They were also found occasionally in hackberry groves.

White-crowned Sparrow (*Zonotrichia leucophrys*). One immature bird was in riparian brush along Sheep Creek on 28 September 1988. Four birds, including two immatures, were in a hawthorne tree along Sheep Creek in the conifer zone the next day.

Golden-crowned Sparrow (*Zonotrichia atricapilla*). This species is found in the fall in the subalpine zone in the Seven Devils Mountains (Larrison et al. 1967).

Dark-eyed Junco (*Junco hyemalis*). At Granite Creek a few flocks were found on three early and late spring trips, and a single bird was there on 9 December 1979. Several small flocks were encountered from Pittsburg Landing to Sheep Creek 13–17 March 1983, and five were along the upper section of Sheep Creek on 27 September 1988. This species occurred in both riparian brush and conifer forest.

Red-winged Blackbird (*Agelaius phoeniceus*). One or two birds were in riparian brush between Brush Creek and Granite Creek in mid-March 1979, and a male bird sang from a lone ponderosa pine tree at the latter creek on 25 March 1979. Two to five birds were in a flooded pasture near Pittsburg Landing on 22 May 1986, and they were also recorded on the July 1986 float trip.

Western Meadowlark (*Sturnella neglecta*). This species was consistently found during all six spring trips into the canyon. Small numbers were singing in open, grassy slopes from the reservoirs down to Pittsburg Landing.

Brewer's Blackbird (*Euphagus cyanocephalus*). A few birds were at a ranch by Pittsburg Landing on 22 May 1986. Flocks of 20 and 40 were seen flying upstream on separate days of the August 1987 float trip, and they were also recorded on the 1986 July float trip.

Brown-headed Cowbird (*Molothrus ater*). A male bird was displaying from some brush at the upper landing at Pittsburg Landing on 22 May 1986; others were recorded on the July 1986 float trip.

Northern Oriole (*Icterus galbula*). Eight birds were seen in the Granite Creek area 10–15 May 1986. Adults with fledglings were found on a July 1986 float trip. Six different birds were found on a 6-km hike upstream from Pittsburg Landing on 22 May 1986.

Rosy Finch (*Leucosticte arctoa*). This species has been recorded in July from the Seven Devils Mountains (Larrison et al. 1967).

Cassin's Finch (*Carpodacus cassinii*). One male was singing in ponderosa pine forest at the saddle leading into Pittsburg Landing on 13 March 1983.

Red Crossbill (*Loxia curvirostra*). A couple of birds were heard singing in ponderosa pine forest at the saddle above Pittsburg Landing on 13 March 1983.

American Goldfinch (*Carduelis tristis*). At Granite Creek two flocks of about 20 individuals each were seen 20 March 1981, and 3 birds were found there on 14 March 1984. Individuals or small flocks were heard or seen floating at several places from Tyron Creek downstream to Robinson Gulch on 25 August 1987, and they were also recorded on the July 1986 float trip.

Evening Grosbeak (*Coccothraustes vespertinus*). At Granite Creek one bird was calling from riparian brush on 9 April 1980, and 8 birds flew past the next day. There were small groups here on 14–16 March 1984, and a flock of 22 birds was in some hackberry trees along the Snake River near Brush Creek on 17 March 1984. Five grosbeaks were in conifers near the top of Stormy Point Trail on 27 September 1988.

House Sparrow (*Passer domesticus*). This species was recorded on the July 1986 float trip.

DISCUSSION

The lack of extensive work through all the seasons precludes any in-depth analysis of Hells Canyon avifauna. A few relevant observations were made, however. First it appears that this part of the Snake River is little used by water birds, except for some diving ducks and Spotted Sandpipers. At least some waterfowl navigate down the river in spring, and possibly Canada Geese and Common Mergansers breed along the river. Shorebirds, except for Spotted Sandpipers, appear to avoid the canyon almost completely. The only other shorebirds seen in late August, a time of major migration through Idaho (Burleigh 1972, personal observation), were a lone Killdeer and a flock of Western Sandpipers flying north. At least some land birds may migrate through the canyon, as indicated by the large flock of American Robins and other small flocks of passerines found in spring and fall. In late September along Sheep Creek nearly all passerines encountered were 2 km or more up the trail above the Snake River. These birds may have been avoiding the hot, dry canyon bottom. Several species, such as Mountain Chickadee, Dark-eyed Junco, and Golden-crowned Kinglet, which breed in conifer forests in Idaho (Burleigh 1972), were found in the canyon bottom in winter and early spring.

Many other species of birds are certain to occur in Hells Canyon, and extensive surveys of the various habitats, especially in early summer and the fall, would greatly increase our knowledge of the canyon's avifauna.

Acknowledgments

I thank Dr. S. C. Taylor, A. C. Taylor, J. S. Taylor, M. Settel, M. Vrdis, S. Jacobs, and P. Warshall for sharing their records with me. The James Henry River Expeditions allowed me an opportunity to float the entire length of the free-running canyon. B. Tershy and D. Breese helped in preparing the manuscript.

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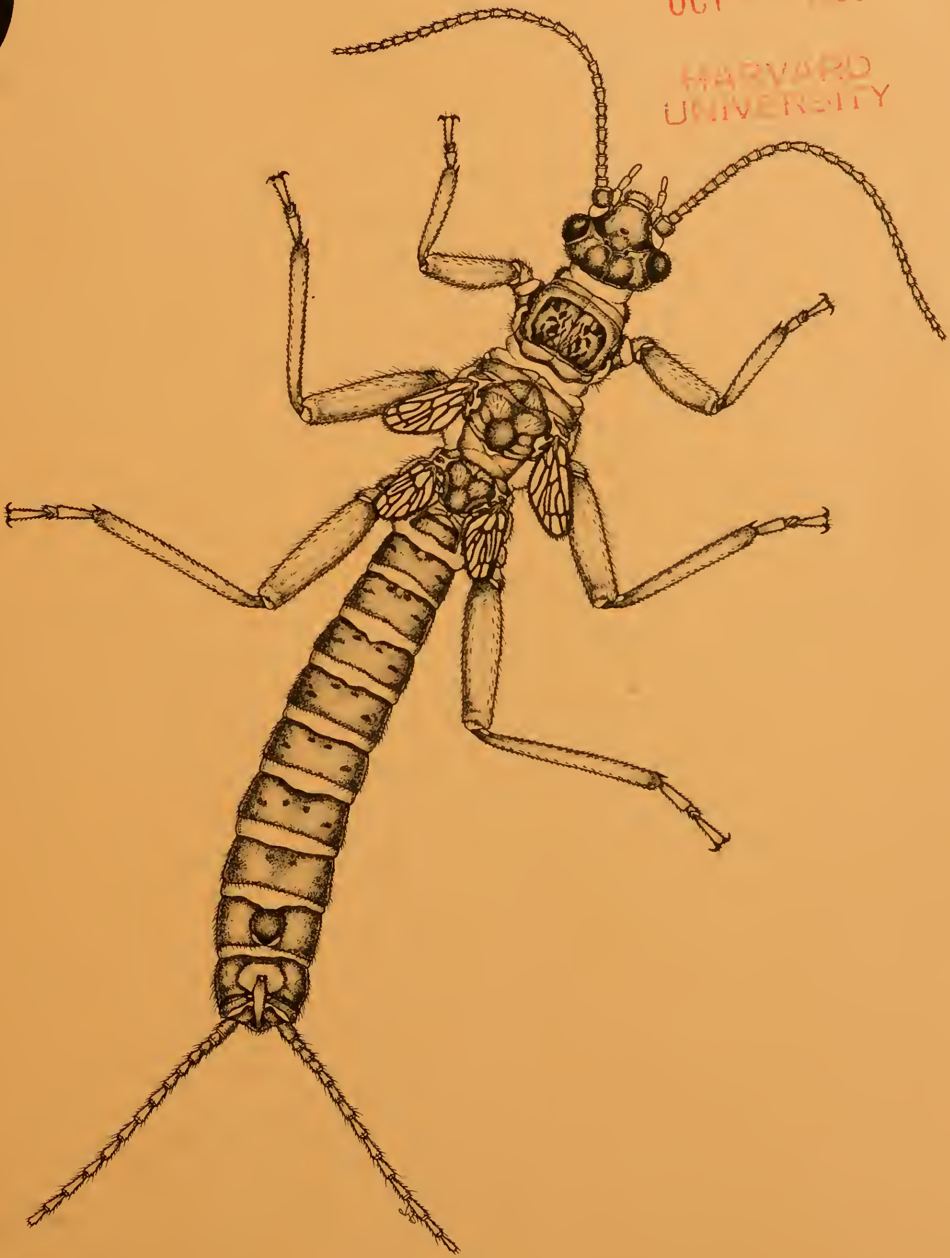

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8-89 650 42168

ISSN 017-3614

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 49 31 July 1989 No. 3

SYSTEMATICS AND DISTRIBUTION OF THE WINTER STONEFLY GENUS *CAPNIA* (PLECOPTERA: CAPNIIDAE) IN NORTH AMERICA

C. Riley Nelson[1] and Richard W. Baumann[1]

ABSTRACT.—The genus *Capnia* in North America is reviewed and compared to other genera in the family. The genus is divided into 10 species groups. A key to the 51 species of *Capnia* in North America is given along with a listing of type localities, type repositories, diagnoses, and distributions. New illustrations of structures bearing characters important for identification and classification are presented. An annotation of the list of *Capnia* of North America given by Stark, Szczytko, and Baumann (1986) reflecting current generic placement of species is produced. From this list *Capnia bakeri* and *sugluka* are moved to *Mesocapnia*. *Capnia barbata* Frison is placed in synonymy under *Capnia decepta*. The movement of *cygna* (synonym of *venosa*), *elevata*, *fibula*, *manitoba*, *venosa*, and *wanica* to *Capnura* (Nelson and Baumann, 1987b) is noted. *Capnia disala* and *ensicala* are placed in *Paracapnia*.

The genus *Capnia* Pictet in North America consists of 51 species that may be divided into 10 morphologically defined species groups and a number of unplaced species. Pictet (1841) erected the genus *Capnia* to include his *Perla nigra* and *Capnia* (*Gripopteryx*) *cancellata*, *Semblis pygmaea* Burmeister, and *S. gracilis* Burmeister. Enderlein (1909) designated *C. nigra* as the type species of *Capnia* and accorded *Gripopteryx* generic status.

The history of North American species placed in *Capnia* begins with Banks's (1897) description of *Arsapnia decepta* based on material from Fort Collins, Colorado. Claassen (1924) synonymized *Arsapnia* under *Capnia*. Banks (1900) described *Capnura venosa*, and Hanson (1946) transferred it to *Capnia*. Nelson and Baumann (1987b) resurrected the genus *Capnura* to include *C. venosa*, *C. elevata*, *C. fibula*, *C. manitoba*, *C. wanica*, and two new species: *C. anas* and *C. intermontana*. Other significant works and workers dealing with the systematics and distribution of *Capnia* in North America are cited in the synonymies of the individual species given below.

An examination of types of most North American species of *Capnia* revealed that certain species currently placed in *Capnia* better fit into other genera, as they are presently understood. Many species listed in *Capnia* in publications prior to 1986 are placed in different genera (often former subgenera) in Stark, Szczytko, and Baumann (1986). The following are annotations of the *Capnia* listed in Stark, Szczytko, and Baumann (1986), given in the order of their list (alphabetical by species):

Mesocapnia bakeri (Banks, 1918), originally described in *Arsapnia*; later moved to *Capnia* by Needham and Claassen (1925). Holotype examined, in MCZ. The holotype, a female, has the projection of the posterior margin of the subgenital plate, characteristic of *Mesocapnia*.

Capnia barbata Frison; placed in synonymy with *Capnia decepta* in this paper. Holotype examined, in INHS.

Capnura cygna (Jewett), originally described in *Capnia*; placed in synonymy with *Capnura venosa* (Banks) by Nelson and Baumann (1987b). Holotype examined, in CAS.

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[1] Life Science Museum, Brigham Young University, Provo, Utah 84602.

Paracapnia disala (Jewett), originally described in *Capnia*; moved to *Paracapnia* by present designation. Holotype examined, in CAS. The holotype, a female, has lateral incisions separating the subgenital plate from the remainder of sternum 8, characteristic of *Paracapnia*. Additional male and female specimens collected from the type locality of Parker Creek, on Marys Peak in Benton Co., Oregon, support the transfer of this species.

Capnura elevata (Frison), originally described in *Capnia*; later moved to *Capnura* by Nelson and Baumann (1987b). Holotype examined, in INHS.

Paracapnia ensicala (Jewett), originally described in *Capnia*; moved to *Paracapnia* by present designation. Holotype examined, in CAS. The holotype, a male, has the base of the epiproct arching posteriorly in a narrow tube as in males of other species in the genus *Paracapnia*. This species is unique in having an irregular lateral expansion on the right side of the epiproct. This expansion appears to be a deformity. Additional specimens from the type locality (Washington, Thurston Co., Boston Harbor, 9 mi north Olympia, 3 January 1959, H. Hacker) are desirable to see if this irregularity is a deformity or a normal feature of the species.

Capnura fibula (Claassen), originally described in *Capnia*; later moved to *Capnura* by Nelson and Baumann (1987b). Holotype examined, in CU.

Capnura manitoba (Claassen), originally described in *Capnia*; later moved to *Capnura* by Nelson and Baumann (1987b). Holotype examined, in CNC.

Mesocapnia sugluka Ricker, originally described in *Capnia*; moved to *Mesocapnia* by present designation. Holotype examined, in CNC. The holotype, a female, has the projection of the posterior margin of the subgenital plate, characteristic of *Mesocapnia*.

Capnura venosa Banks; later moved by Hanson (1946) to *Capnia*. This species was returned to *Capnura* by Nelson and Baumann (1987b) and is the type-species of the genus. Holotype examined, in MCZ.

Capnura wanica (Frison), originally described in *Capnia*; later moved to *Capnura* by Nelson and Baumann (1987b). Holotype examined, in INHS.

Significant morphological differences exist in male and female terminalia between the type of the genus, *Capnia nigra* Pictet from Europe, and those species currently assigned to *Capnia* in North America. These differences are of the magnitude that many students of Plecoptera would recognize as generic-level, when compared to other groups of stoneflies. Separate genera may be useful in the division of this large plecopteran genus. Any division, however, should occur after a careful study of the genera on a worldwide scope to avoid problems of usage among workers in the Nearctic and the Palearctic regions.

North American members of the genus *Capnia* (sensu lato) may be divided into 10 monophyletic groups and an eleventh category that consists of species of uncertain placement. This last group contains several distinct subgroups and is undoubtedly polyphyletic. Further study of the generic status of *Capnia* as it relates to the genera of the world should help in classifying these enigmatic species. The groups in *Capnia* are defined using characters of the male terminalia and are generally supported by characters of the female subgenital plate.

MATERIALS AND METHODS

Collections of capniids from northern and western North America were borrowed from those individuals and institutions listed in the acknowledgments. Type localities or nearby sites were visited by the authors to obtain fresh specimens for as many species as possible. Fresh collections of 47 of the 51 species were obtained during collecting trips taken by the authors and various members of the Winter Stonefly Club.

Specimens of Capniidae are easiest to identify when collected and stored in 70% alcohol. Those specimens collected and curated by Claassen from 1920 to 1940 were usually adequately preserved. Alcohol specimens stored in cool environments were in much better condition than those that had experienced extreme heat. Specimens are in best condition when few individuals are placed in each vial. A rule of thumb used to ensure proper preservation is that a rough ratio of 4 parts alcohol to 1 part insect be maintained in storage vials.

Pinned, dried specimens were also examined. These specimens were prepared for viewing by removing the abdomen and relaxing it in a dilute solution of sodium phosphate tribasic. After the relaxed abdomen was viewed, it was placed in a plastic genitalia vial containing glycerin and pinned with the remainder of the specimen.

Specimens were examined and identified using a Wild M5 dissecting stereomicroscope and a Swift compound stereomicroscope. Selected specimens were prepared and viewed using an AMray scanning microscope following procedures outlined in Nelson and Baumann (1987a). Drawings were made using a camera lucida attachment on a Wild M8 dissecting microscope and consulting the scanning electron micrographs.

Much collecting of these interesting stoneflies has been done in the past; well over 20,000 specimens in the genus *Capnia* were examined during this study to determine species distributions. Several thousand specimens in related genera were examined as well to note variations in different genera. Several terms used in the keys are defined as follows: horns are lateral projections of the epiproct usually found on the distal third; they may be far from the tip as in *C. barberi* (Figs. 7, 8) or near the tip as in *C. decepta* (Figs. 35, 36). The neck of the epiproct is the narrow junction between the epiproct and the abdomen; often this area is constricted, separating the gibbous bulb of the epiproct from the main body. Compoundly curved refers to the sinuous shape of the epiproct, which curves forward, dips downward, and then returns upward (Figs. 40, 104). Sensillae are defined as simple sense organs or parts of compound sense organs. In this work they represent the setae and other projections of the tergal knobs of the abdomen (Fig. 174). Further terminology regarding morphology of capniids used in this study is given under the Decepta group, in Figures 209, 210, and in Nelson and Baumann (1987a–c).

Records of all specimens studied were kept. Available label data including state or province, county, locality, collecting date, and collectors, as well as any other miscellaneous information, were recorded. The detailed label information is recorded by species in log books in the possession of the senior author; a computer listing of these records is deposited in the insect collection of the M. L. Bean Life Science Museum at Brigham Young University.

Type repositories are listed in parentheses at the end of the holotype section of individual species treatments. The minimum number of specimens examined by the authors is given in parentheses at the end of the individual distribution sections. The seasonal distribution of each species is given as a range of the earliest to latest collecting dates following the number of specimens examined by the authors. This range of dates represents all collections of a given species throughout its geographical range. In general, *Capnia* emerge earliest at lower elevations and southerly latitudes and emerge progressively later as elevation increases or as one proceeds north.

The following abbreviations are used in this text: CAS—California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118. CNC—Canadian Nation Collection, Biosystematics Research Centre, Ottawa, Ontario, Canada, K1A 0C6. Co.—County. CU—Cornell University, Ithaca, NY 14853. INHS—Illinois Natural History Survey, 607 East Peabody, Champaign, IL 61820. LACM—Los Angeles County Museum, Exposition Park, Los Angeles, CA 90007. MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138. USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

SYSTEMATICS SECTION

Capnia Pictet

Capnia Pictet 1841: 320. Claassen 1924: 43, 1931: 109, 1940: 91. Needham and Claassen 1925: 253. Hanson 1943b: 158, 1946: 229. Jewett 1956: 169, 1959: 42, 1960: 143. Illies 1966: 130. Zwick 1973: 370. Ricker and Scudder 1975: 338. Baumann, Gaufin, and Surdick 1977: 61. Harper and Stewart, 1984: 227. Stark, Szczytko, and Baumann 1986: 385.

Arsapnia Banks 1897: 22, 1907a: 15. Claassen 1924: 43.

DIAGNOSIS.—Winged forms of *Capnia* may be separated from those of *Eucapnopsis*, *Isocapnia*, *Nemocapnia*, and *Paracapnia* by R_1 of the wing curving anteriorly at the origin and recurving posteriorly to produce a curve near its origin. R_1 is flat in the latter three genera, not curving anteriorly near its origin. Males of *Capnia* are separated from those of *Bolshecapnia* by the absence of a sternal vesicle on sternum 9 and from *Utacapnia* by the lack of a laterally forked upper limb or limb remnant on the epiproct. *Allocapnia* males have an epiproct consisting of two limbs while *Capnia* males generally have a single-limbed epiproct (exceptions are *C. nearctica* and *C. valhalla*, which have a longer portion at the tip of the lower limb forming a curve, and *C. spinulosa*, which has the two limbs closely appressed). Males of *Mesocapnia* are morphologically distinct from *Capnia* in having a sharp, pointed spine at the apex of the epiproct; specimens of *Mesocapnia* may be identified using Baumann and Gaufin (1970). The presence of a lower limb of the epiproct, which is not appressed to the upper limb, serves to separate the males of *Capnura* from those of *Capnia*. This lower limb in *Capnura* may be strongly reduced such as in *C. wanica*, half as long as the upper limb as in *C. elevata*, or fully as long as the upper limb as in *C. manitoba*. Any vestige of a lower limb is absent in most *Capnia*, although a long lower limb appressed to the upper limb is present in *C. nearctica*, *C. spinulosa*, and *C. valhalla*. These three species are currently left in *Capnia* even though they show phylogenetic affinities diverging from the rest of the genus. A detailed study comparing the remainder of the North American species to these three should provide valuable information regarding the phylogenetics of *Capnia* and other capniid genera. Generic placement of these three species awaits a revision of the genera of the world since they bear closer affinities to other species in the Palearctic, including *Capnia nigra*, than to other North American members of the genus.

Females of *Utacapnia* may be separated from those of *Capnia* by the presence of a darkened projection on the posterior margin of the subgenital plate. This projection is often split into two or more short lobes. The females of *Bolshecapnia*, *Mesocapnia*, and *Capnia* are difficult to separate by any simple characterization, but in general the subgenital plate of *Capnia* is more heavily sclerotized and darkened, especially near the posterior margin. Most females of *Mesocapnia* have a subgenital plate that narrows to a point on the posterior margin. This narrowed area of the plate in *Mesocapnia* is concolorous with the remainder of the plate; species of *Capnia* that have a narrowed posterior margin of the subgenital plate also have a darkened color pattern on the plate (Fig. 220). The presence of a light medial area (often with an imbedded Y-shaped sclerite) on the subgenital plate of females of *Capnura* serves to distinguish females of this genus from *Capnia*.

DISTRIBUTION.—In North America species in this genus inhabit streams from the Atlantic coast of Quebec to the shores of the Pacific in Alaska (Fig. 280). They are distributed from the north slope of the Brooks Range in Alaska and streams draining into Ungava Bay in northern Quebec to the isolated mountain islands of southern Arizona, California, and northwestern Mexico. They are absent from most of the Great Plains east of the Rocky Mountains in the United States but occur further east on the prairies of Manitoba and Saskatchewan in Canada.

The largest number of species inhabit the streams of the Cascade Mountains, Sierra Nevada, and Rocky Mountains. Two species, *C. vernalis* and *C. confusa*, are responsible for the broad distributional range of the genus; however, most species in the genus have a much narrower range, often limited to a single mountain mass within one of the larger mountain systems. Several species of *Capnia* have been described from very limited material from a single locality.

Capnia Species-Groups

The genus *Capnia* can be divided into 10 species-groups (Table 1), each supported by one or more synapomorphies (Nelson, unpublished data and summarized in the beginning of the individual species-group sections). The characters used to differentiate the groups in the following key are a subset of these synapomorphies. The following key will also aid in the identification of the several species of *Capnia* not placed in the various species-groups. A couplet separating the genus *Mesocapnia* is included for convenience; species in this group can be identified using Baumann and Gaufin (1970). An analysis of the phylogenetics of the genus, its groups, and their relationships to other genera in the family is underway and will be published at a future date. Preliminary results lead us to believe that the group concepts used in this publication will be the same as that of a more detailed phylogenetic analysis that is planned. It should be noted that the key to the males is more compact and concise (when compared to that of the females) because more unambiguous characters are available for the males than the females. No attempt is made to provide a key to the nymphs; current concepts used to differentiate capniid nymphs even at the generic level are most inadequate. Further comparative morphological studies of capniid nymphs is necessary to screen the variety of characters currently used to separate genera for taxonomic utility.

Key to Males of Species Groups and Unassigned Species of *Capnia*

1. Epiproct composed of two appressed limbs (Figs. 108, 164, 188) 2
— Epiproct composed of a single limb that is sometimes partially divided near apex 4

TABLE 1. Groups of Capnia

Barberi Group
1. *Capnia barberi* Claassen
2. *C. hornigi* Baumann & Sheldon
3. *C. mono* Nelson & Baumann
4. *C. palomar* Nelson & Baumann
5. *C. shepardi* Nelson & Baumann
6. *C. yosemite* Nelson & Baumann

Californica Group
7. *Capnia californica* Claassen
8. *C. jewetti* Frison
9. *C. ophiona* Nelson & Baumann
10. *C. quadrituberosa* Hitchcock
11. *C. regilla* Nelson & Baumann
12. *C. saratoga* Nelson & Baumann
13. *C. umpqua* Frison
14. *C. ventura* Nelson & Baumann

Coloradensis Group
15. *Capnia coloradensis* Claassen
16. *C. hitchcocki* Nelson & Baumann
17. *C. petila* Jewett

Decepta Group
18. *Capnia arapahoe* Nelson & Kondratieff
19. *C. coyote* Nelson & Baumann
20. *C. decepta* (Banks)
21. *C. pileata* Jewett
22. *C. sequoia* Nelson & Baumann
23. *C. teresa* Claassen
24. *C. tumida* Claassen
25. *C. utahensis* Gaufin & Jewett

Excavata Group
26. *Capnia cheama* Ricker
27. *C. excavata* Claassen
28. *C. uintahi* Gaufin

Gracilaria Group
29. *Capnia elongata* Claassen
30. *C. gracilaria* Claassen
31. *C. lacustra* Jewett
32. *C. promota* Frison

Mariposa Group
33. *Capnia giulianii* Nelson & Baumann
34. *C. inyo* Nelson & Baumann
35. *C. mariposa* Nelson & Baumann

Nana Group
36. *Capnia glabra* Claassen
37. *C. licina* Jewett
38. *C. melia* Frison
39. *C. nana* Claassen
40. *C. oregona* Frison
41. *C. willametta* Jewett

Nearctica Group
42. *Capnia nearctica* Banks
43. *C. valhalla* Nelson & Baumann

Vernalis Group
44. *Capnia confusa* Claassen
45. *C. lineata* Hanson
46. *C. vernalis* Newport

Species of uncertain group status
47. *Capnia scobina* Jewett
48. *C. sextuberculata* Jewett
49. *C. spinulosa* Claassen
50. *C. zukeli* Hanson

Species of uncertain taxonomic status
51. *Capnia erecta* Jewett

2(1). Epiproct with both limbs tightly appressed along entire length, lower limb not curving away from upper apically (Fig. 164) .... *spinulosa* Claassen

— Epiproct with lower limb separated from upper near apex, tip of lower limb curving upward then downward .... Nearctica Group (page 336) 3

3(2). Base of epiproct strongly constricted (Fig. 187), arched portion of lower limb about half as long as epiproct (Fig. 188) .... *valhalla* Nelson & Baumann

— Base of epiproct broadly joined to abdomen (Fig. 107), arched portion of lower limb about one-third length of epiproct (Fig. 108) .... *nearctica* Banks

4(1). Male abdominal terga bearing paired hooked knobs on segments 6–8 (Figs. 153, 154) .... *sextuberculata* Jewett

— Male terga with fewer knobs (may be absent), never on all three listed segments (Figs. 14, 26, 66, 70) 5

5(4). Paired tergal knobs present on segments 8 or 9 or both (Figs. 14, 66, 190) or on segments 5 and 6 (*C. jewetti*, Fig. 70) 6

— Paired tergal knobs absent from segments 5, 6, and 8, 9 (Figs. 26, 194), although a single medial knob may be present on one or more of these segments; or if paired knobs present on 9, tergum 7 also bearing knob (Figs. 5, 117) 7

6(5). Epiproct with anteapical dorsomedial membranous area (Figs. 11, 15, 71, 111, 135, 139, 143, 179, 191); epiproct bulbous, consisting of two processes in lateral view (Fig. 192); lateral horns of epiproct absent... Californica Group (page 302)

— Epiproct with membranous area apical (Figs. 47, 67, 87); epiproct not bulbous, consisting of a single lobe; short lateral horns of epiproct usually present (absent in *C. inyo*) .... Mariposa Group (page 328)

7(5). Tergum 7 or tergum 8 bearing medial knob of various sizes (Figs. 5, 21, 33, 97; small in *C. hitchcocki*, Fig. 57) 8

— Terga 7 and 8 lacking medial knob 13

8(7). Epiproct tip hanging downward (Figs. 24, 60, 124) .... Coloradensis Group (page 308)

— Epiproct tip horizontal or curving upward (Figs. 28, 52, 56) 9

9(8). Tergum 8 with highly modified knob bearing setae (Figs. 18, 42, 102) 10

— Tergum 8 without medial knob 11

10(9). Epiproct with broad lateral flange; knob on tergum 8 forming cowl that covers tip of epiproct to lateral flange in unrelaxed specimens (Figs. 19, 43, 175) . . . . Excavata Group (page 320)

— Epiproct without lateral flange, only slightly expanded laterally (Figs. 99, 199); knob on tergum 8 less prominent . . . . Nana Group (page 330)

11(9). Epiproct long and tubelike, not highly gibbous in lateral view (Figs. 40, 56, 76, 132); knob on tergum 7 often low, only slightly modified with few sensillae (well developed in *C. elongata*, absent in *C. lacustra*); horns absent from apex of epiproct . . . . Gracilaria Group (page 322)

— Epiproct shorter, bulbous in either lateral or dorsal views or both (Figs. 8, 35, 36); knob on tergum 7 well developed (less so in *C. utahensis*); lateral horns present on tip of epiproct 12

12(11). Tergum 9 divided and bearing prominent sensillae; epiproct not greatly broadened laterally (Figs. 7, 63, 95, 119, 159, 203); horns not on extreme apex of epiproct, but located near gibbosity . . . . Barberi Group (page 296)

— Tergum 9 divided but not modified to bear sensillae; epiproct greatly broadened laterally (Figs. 31, 35, 127, 151, 176, 171, 183; narrow in *C. arapahoe*, Fig. 3); horns short and appressed to extreme apex of epiproct . . . . Decepta Group (page 310)

13(7). Epiproct directed posteriorly, not recurved over abdomen (may be a malformed specimen, known only from holotype) . . . . *erecta* Jewett

— Epiproct recurved over abdomen in usual fashion 14

14(13). Epiproct with tip modified into a sharp spine . . . . *Mesocapnia* Rauser

— Epiproct with tip blunt 15

15(14). Epiproct bending to the left in dorsal view (Fig. 147) and armed with short, heavy spines . . . . *scobina* Jewett

— Epiproct oriented on midline of abdomen in dorsal view, lacking spination on shaft 16

16(15). Epiproct bending sharply near base in lateral view (Fig. 76); adults known only from deep in Lake Tahoe . . . . *lacustra* Jewett

— Epiproct curving evenly near base; adults caught near large rivers, small streams, and lake margins 17

17(16). Epiproct more than 15 times as long as high in lateral view (Fig. 208); wings of male short . . . . *zukeli* Hanson

— Epiproct less than 15 times as long as high in lateral view (Figs. 28, 84, 196); wings of male short or long . . . . Vernalis Group (page 338)

Key to the Females of *Capnia*

(*arapahoe*, *erecta*, *giulianii*, *ophiona*, and *willametta* unknown)

1. Subgenital plate externally dark, heavily sclerotized, contrasting with remainder of sternum 8 (Figs. 211, 215, 218) 2

— Subgenital plate lighter (Figs. 222, 229, 256), if dark then darkness diffuse, coming from internal structures (Fig. 234) 14

2(1). Dark area of plate wide, 0.4–0.8 width of sternum 8; dark area usually as wide as long (Figs. 230, 232) 3

— Dark area of plate narrower 0.2–0.35 width of sternum 8; dark area longer than wide (Figs. 215, 248, 250) 8

3(2). Hind margin of plate with medial area either produced (Fig. 220) or notched (Fig. 249) posteriorly 4

— Hind margin of plate entire, medial posterior margin area not produced or notched but broadly rounded 5

4(3). Medial area of plate produced posteriorly as an angular extension, not notched (Fig. 220) . . . . *excavata*

— Medial area of posterior margin of plate notched broadly, not produced posteriorly (Fig. 249) . . . . *teresa*

5(3). Sterna 7 and 8 broadly joined by sclerotized bridge yielding continuous sclerite (Fig. 219) . . . . *elongata*

— Sterna 7 and 8 separated by membrane, if joined then anterior part of sternum 7 membranous or at least color contrasting greatly with posterior part and sternum 8 (Figs. 211, 230, 254) 6

6(5). Darkest area of subgenital plate triangular (Fig. 254) . . . . *valhalla*

— Darkest area of subgenital plate quadrate (Figs. 211, 230) 7

7(6). Internal sclerotization of vagina visible through subgenital plate, forming a rough trapezoid . . . . Coloradensis Group (page 308)

— Internal sclerotization of vagina obscured by very dark subgenital plate . . . . Barberi and Mariposa Groups (pages 296, 328)

8(2). Medial dark area of plate narrow, width 0.2 (or less) of segment 8, posterior margin angularly produced rearward (Fig. 248) 9

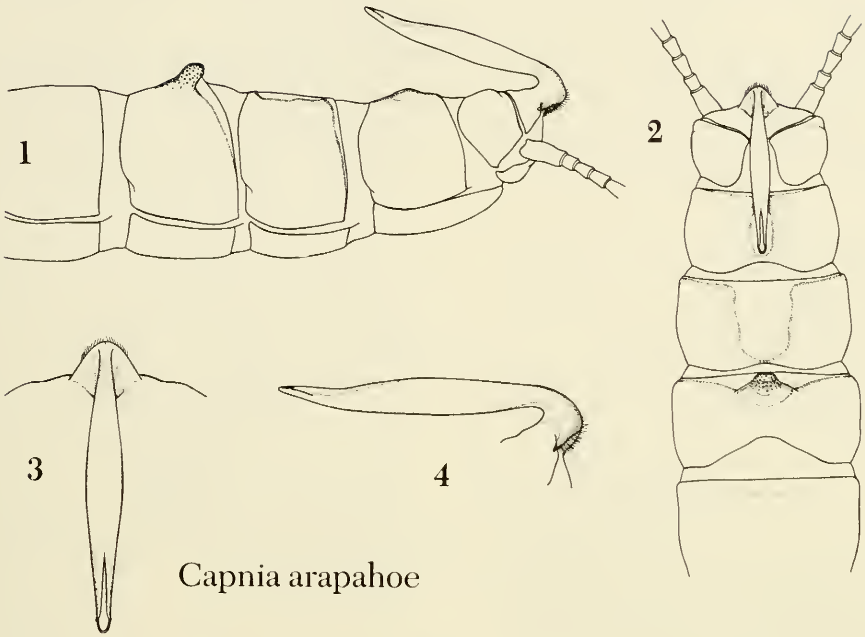
— Medial dark area of plate wider, 0.25–0.35 width of segment 8, posterior margin entire, not greatly produced rearward in angular flap 11

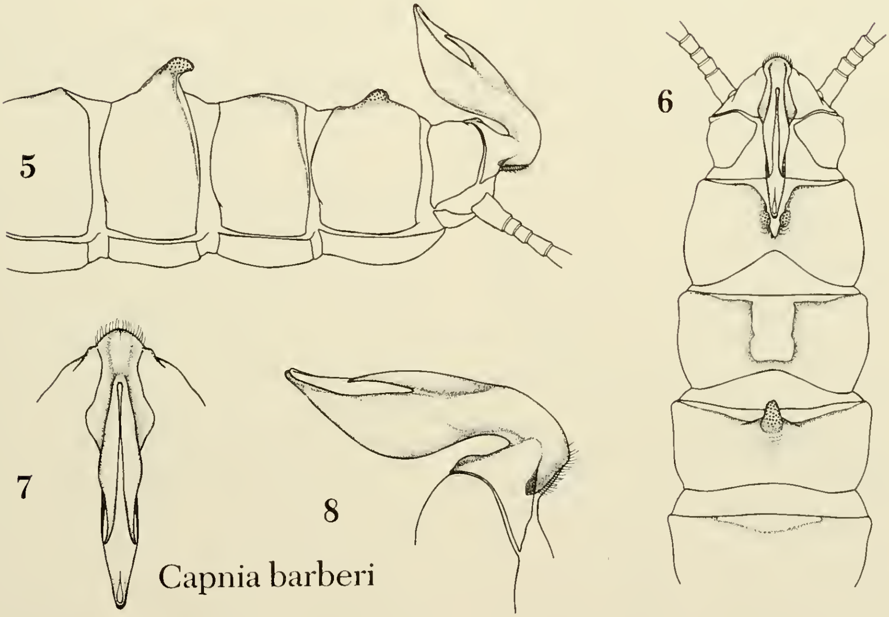
9(8). Posterior margin of subgenital plate evenly rounded, not extending medially with an angulate or notched projection (Fig. 254) . . . . . *valhalla*

— Posterior margin of subgenital plate extending medially with an angulate or notched projection (Figs. 235, 248) 10

10(9). Medial dark area of subgenital plate notched posteriorly, dark color not extending anteriorly to margin of sternum 8 (Fig. 235) . . . . *nearctica*

— Medial dark area of subgenital plate not notched posteriorly, dark color extending anteriorly to margin of sternum 8 as a narrow band (Fig. 248) . . . . *spinulosa*





Figs. 1–4. *Capnia arapahoe* Nelson & Kondratieff: 1, male terminalia, lateral; 2, male terminalia, dorsal; 3, male epiproct, dorsal; 4, male epiproct, lateral. Colorado, Larimer Co., Young Gulch above Ansel Watrous Campground, 22 March 1986, B. C. Kondratieff.

Figs. 5–8. *Capnia barberi* Claassen: 5, male terminalia, lateral; 6, male terminalia, dorsal; 7, male epiproct, dorsal; 8, male epiproct, lateral. California, Plumas Co., Long Valley Creek, Hwy 70, Cromberg, 14 February 1985, R. W. Baumann and C. R. Nelson.

11(8). Internal sclerotization visible through plate; plate with origins in membrane between sterna 7 and 8, notched laterally in basal one-fourth (Figs. 215, 238) . . . . Coloradensis Group (except *hitchcocki*) (page 308)

— Internal sclerotization not visible through plate; plate originating as anterior margin of sternum 8; notches, if present, usually in distal three-fourths (Note: some specimens of *decepta* are laterally notched in basal one-fourth, but the plate is usually broader than that of *coloradensis.*) 12

12(11). Subgenital plate light, not heavily sclerotized, deeply notched on lateral margins to produce hourglass shape (Fig. 246) . . . . *sextuberculata*

— Subgenital plate darker, heavily sclerotized, lateral notches not so deep (Figs. 214, 218) 13

13(12). Posterior margin of plate notched medially, producing pair of sclerotized projections (Fig. 214) . . . . *cheama*

— Posterior margin of plate entire (Fig. 218) . . . . Decepta Group (except *teresa*, which is notched) (page 310)

14(1). Sterna 7 and 8 joined in sclerotized bridge (Fig. 256), or with medial projection on hind margin of sternum 8 (Fig. 216), or with irregular sclerites imbedded near midline between these segments (Fig. 229); hind margin of plate recessed and bearing paired internal sclerotized patches (patches absent in *confusa*, Fig. 216) . . . . Vernalis Group (page 338)

— Sterna 7 and 8 separated, or if joined (*petila*, Fig. 238) then hind margin of plate without heavy internal sclerotization 15

15(14). Hind margin of plate notched medially 16

— Hind margin of plate entire or with medial posterior projection 18

16(15). Hind margin of plate straight except for medial notch (Fig. 249) . . . . *teresa*

— Hind margin of plate angular, continuing evenly from lateral margins with medial apical notch 17

17(16). Angular projection on hind margin of plate broad, with wide, deep notch (Fig. 214) . . . . *cheama*

— Angular projection narrow, notch narrow and shallow (Fig. 235) . . . . *nearctica*

18(15). Hind margin of plate a dark, well-defined, even line (Fig. 221) . . . . *glabra*

— Hind margin of plate variable, darkness, if present, not even and well defined 19

19(18). Hind margin of plate with slight medial posterior projection, often with additional irregular projections (Figs. 219, 222, 227, 240); hind margin often darkened . . Gracilaria Group (page 322)

— Hind margin of plate without projections 20

20(19). Hind margin of plate a heavily sclerotized bar that is uncolored, some species with medial angular flap overhanging this light-colored bar (Figs. 212, 213, 226, 241, 243, 252, 255) . . . . Californica Group (page 302)

— Hind margin of plate either lightly sclerotized and lightly colored or heavily sclerotized and heavily colored, not heavily sclerotized and lightly colored 21

21(20). Hind margin of plate with internal darkening that becomes lighter moving anteriorly and medially, resulting in a dark triangle with a lighter apex directed anteriorly (Figs. 221, 228, 231, 233, 234, 236, 254) . . . . Nana Group (page 330) and *valhalla*

— Hind margin of plate not darkened, about same color as anterior margin 22

22(21). Darkening of subgenital plate resembling hourglass (Fig. 246) . . . . *sextuberculata*

— Darkening of subgenital plate not resembling hourglass 23

23(22). Sterna 7 and 8 joined medially; hind margin of plate with slight medial projection (Fig. 238) . . . . *petila*

— Sterna 7 and 8 separate; hind margin of plate straight, recessed anteriorly from hind margin of lateral sclerites of segment 8 24

24(23). Length 9 mm; inhabiting streams on west central border of Idaho (Latah Co.); subgenital plate as in Fig. 258 . . . . *zukeli*

— Length 6–7 mm; not in streams of western Idaho 25

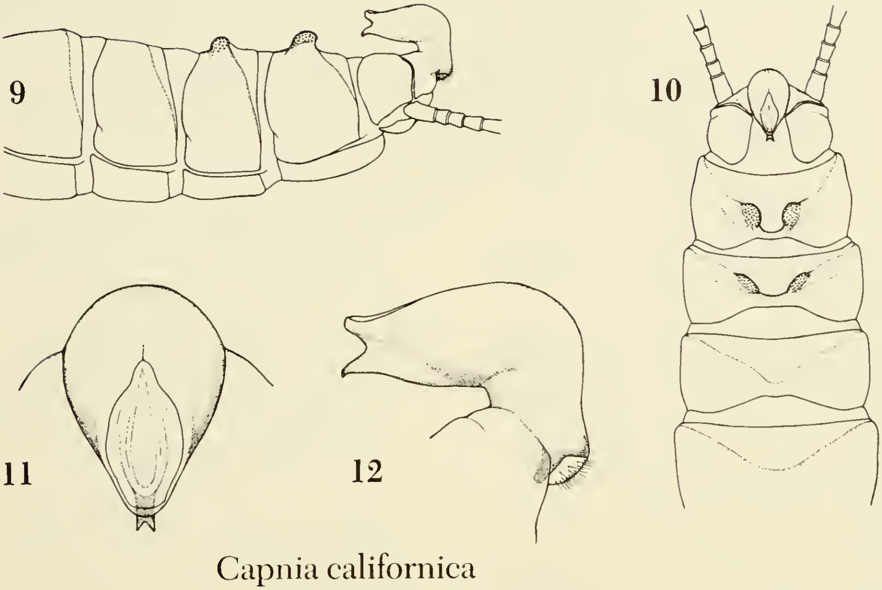
25(24). Inhabiting streams of Lake Tahoe area in east central California . . . . *scobina*

— Inhabiting streams of central Rocky Mountains and mountains of eastern Great Basin . . . . *uintahi*

Barberi Group

This group is unified by the presence of a tergal knob on segment 7, a pair of tergal knobs on segment 9, the presence of rather short lateral horns located some distance from the apex of the epiproct, and an extensive membranous portion of the epiproct dorsally that extends over one-half the length of the epiproct. The females in the group have a broad, heavily colored and sclerotized subgenital plate that often bulges ventrally. Some of the species of the group have females that have the subgenital plate joined by a broad band of sclerotization to sternum 8. The species included in this group are *C. barberi* Claassen, *C. hornigi* Baumann & Sheldon, *C. mono* Nelson & Baumann, *C. palomar* Nelson & Baumann, *C. shepardi* Nelson & Baumann, and *C. yosemite* Nelson & Baumann.

DISTRIBUTION.—Members of this group are confined to the Sierra Nevada and adjacent mountain ranges from the Mount Lassen area on the north to Palomar Mountain in San Diego County on the south. The White Mountains of western Nevada are home to at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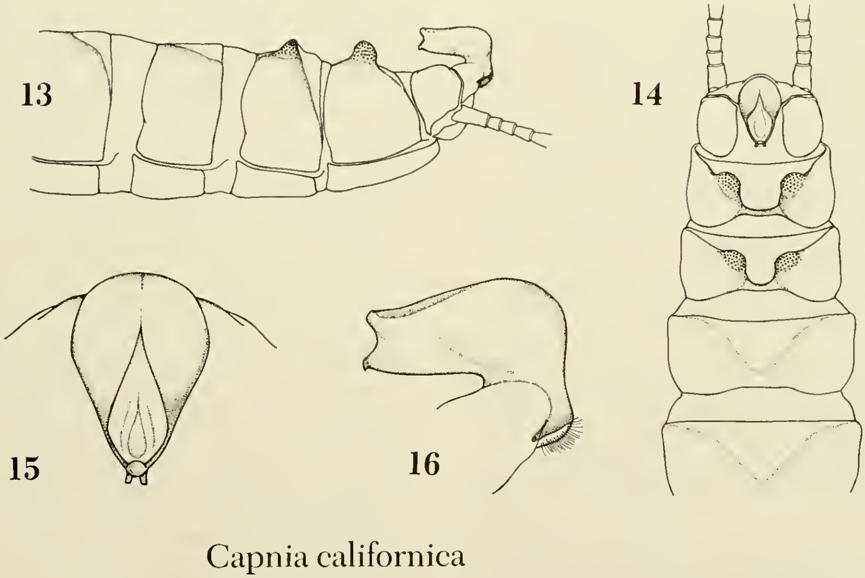
Capnia californica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Capnia californica

Figs. 9–12. *Capnia californica* Claassen: 9, male terminalia, lateral; 10, male terminalia, dorsal; 11, male epiproct, dorsal; 12, male epiproct, lateral. California, Marin Co., Bear Valley Creek, Point Reyes National Seashore, 25 May 1975, D. G. Denning.

Figs. 13–16. *Capnia californica* Claassen: 13, male terminalia, lateral; 14, male terminalia, dorsal; 15, male epiproct, dorsal; 16, male epiproct, lateral. Arizona, Gila Co., Strawberry Creek, Hwy 87, Strawberry, 14 January 1984, R. W. Baumann and C. R. Nelson.

least one of the species of this group (*C. hornigi*). The individual species of this group generally have quite narrow ranges, and further collecting in the future would be desirable to identify the actual limits of the ranges of the species. It is not uncommon to find several of the species in this group occurring sympatrically and synchronously.

Key to the Males of the Barberi Group

1. Lobular free portion of tergal knob on segment 7 broad, greater than one-fourth width of segment (Figs. 94, 158) 2

— Lobular free portion of tergal knob on segment 7 narrow, less than one-tenth width of segment (Figs. 6, 62, 118, 202) 3

2(1). Apex of epiproct truncate; membranous portion of epiproct darkened (Figs. 158, 159) .... *shepardi* Nelson & Baumann

— Apex of epiproct pointed; membranous portion of epiproct light (Figs. 94, 95) .... *mono* Nelson & Baumann

3(1). Epiproct three times as long as high (Fig. 8), horn-bearing ridges of epiproct parallel (Fig. 7) .... *barberi* Claassen

— Epiproct more than three times as long as high, horn-bearing ridges diverging apically (Figs. 64, 119, 204) 4

4(3). Epiproct deeply recurved, horn separated from gibbosity by a curving notch in lateral view (Fig. 204); apex of tergal knob on segment 7 deeply bifid (Fig. 202) ..... *yosemite* Nelson & Baumann

— Epiproct not curving so deeply, horn joining gibbosity at an acute angle; apex of tergal knob unsplit or shallowly split (Figs. 64, 120) 5

5(4). Horn longer, one-fifth length of epiproct in lateral view (Fig. 61); tergal knob on segment 7 strongly lobular, tubercles generally limited to knob (Fig. 62); dorsal membranous area of epiproct broad, extending basally one-half length of epiproct (Fig. 63) .... *hornigi* Baumann & Sheldon

— Horn shorter, one-ninth length of epiproct in lateral view (Fig. 120); tergal knob on segment 7 not as strongly produced, tubercles more diffuse, covering broad area (Fig. 118); dorsal membranous area in large part limited to tip extending basally in a narrow furrow (Fig. 119) .... *palomar* Nelson & Baumann

Key to the Females of the Barberi Group

1. Subgenital plate parallel sided, not becoming narrower distally (Figs. 211, 232, 237) 2

— Subgenital plate with lateral margins converging distally (Figs. 224, 247, 257) 4

2(1). Subgenital plate joined broadly to sternum 7 (as in Fig. 219) .... southern *barberi*

— Subgenital plate separated from sternum 7 by a band of membrane or joined to sternum 7 in a narrow, medial bridge (Figs. 232, 237) 3

3(2). Subgenital plate separated from sternum 7 by a membranous band (Figs. 232, 211) .... *mono*, northern *barberi*

— Subgenital plate joined to sternum 7 by a narrow, medial bridge (Fig. 237) .... *palomar*

4(1). Subgenital plate bulging ventrally forming a hemisphere when viewed laterally ..... *yosemite*

— Subgenital plate may be bulging but not forming a complete hemisphere 5

5(4). Subgenital plate with apparent notches laterally at junction of sternites 7 and 8 (Fig. 247) ... *shepardi*

— Subgenital plate without lateral notches at junction of sternites 7 and 8 (Fig. 224) .... *hornigi*

Capnia barberi Claassen

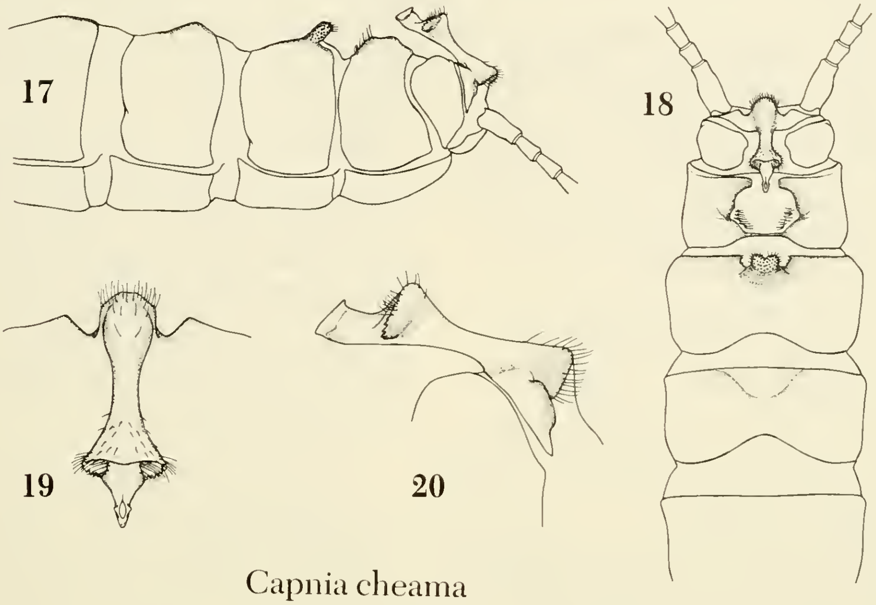
Figs. 5–8, 211, map Fig. 259

Capnia barberi Claassen 1924: 55, 1940: 92. Needham and Claassen 1925: 267. Hanson 1946: 238. Jewett 1956: 169, 1960: 143. Illies 1966: 132. Nebeker and Gaufin 1967a: 418. Sheldon and Jewett 1967: 4. Zwick 1973: 371. Stark et al. 1986: 385.

HOLOTYPE.—Male, California, Plumas Co., Feather River Canyon near Caribou, 24 January 1923, H. S. Barber; (USNM).

DIAGNOSIS.—The male of this species is differentiated from others in the group by the parallel orientation of the horn-bearing sclerites of the epiproct as seen from dorsal view coupled with the horns distant from the apex. The long, narrow horns that are separated from the main body of the epiproct at an acute angle help in segregation of this species from *C. yosemite*, in which the horn connects to the body in a deep, broad notch, and the remaining species in the group which have shorter horns. The females of this species are not readily separated from others in the group. The females occur in two forms, those with a square subgenital plate that originates with the anterior margin of sternum 8 and those with a rectangular plate with origins in the distal third of sternum 7. The square-plated female occurs in all the reported localities except those in the southernmost extensions of the range of the species, such as localities in Tuolumne County. The following description of the female of this species is based on material from the northern portion of its range, near the type locality of the male.

DESCRIPTION.—Female, wing macropterous; forewing 7.2 mm in length; length of body 5.8 mm. Subgenital plate square but with posterior margin irregular, plate heavily sclerotized and darkened, originating at anterior margin of sternum 8; sterna 7 and 8 separated by a distinct intersegmental membrane;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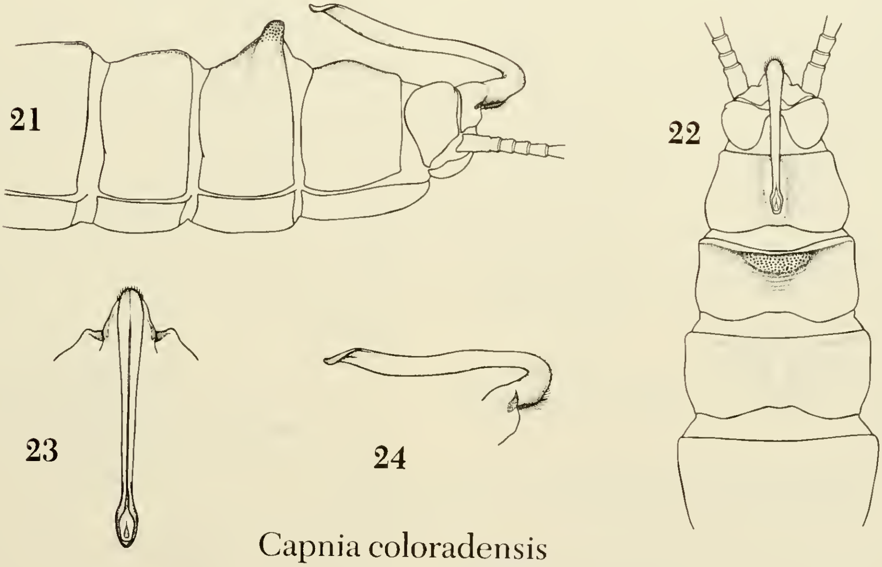
Capnia cheama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Capnia coloradensis

Figs. 17–20. *Capnia cheama* Ricker: 17, male terminalia, lateral; 18, male terminalia, dorsal; 19, male epiproct, dorsal; 20, male epiproct, lateral. Montana, Lincoln Co., Kootenai River, 19 March 1970, R. L. Newell.

Figs. 21–24. *Capnia coloradensis* Claassen: 21, male terminalia, lateral; 22, male terminalia, dorsal; 23, male epiproct, dorsal; 24, male epiproct, lateral. Colorado, Routt Co., Willow Creek near Hahns Peak, 13 May 1968, B. R. Oblad.

posterior margin of sternum 7 lightly sclerotized, anterior portion of segment more or less membranous.

MATERIAL.—Female, California, Plumas Co., Long Valley Creek, Highway 70, Cromberg, 14 February 1985, R. W. Baumann and C. R. Nelson; (BYU).

DISTRIBUTION.—CALIFORNIA: Alpine Co.; El Dorado Co.; Nevada Co.; Placer Co.; Plumas Co.; Shasta Co.; Sierra Co.; Tehama Co.; Tuolumne Co. NEVADA: Washoe Co.; (1440). 9 December–24 June.

Capnia hornigi Baumann & Sheldon

Figs. 61–64, 224, map Fig. 260

Capnia hornigi Baumann & Sheldon 1984: 30. Stark et al. 1986: 385.

HOLOTYPE.—Male, #76499 (and female allotype), Nevada, Esmeralda Co., White Mountains, Middle Creek, 10 February 1977, A. L. Sheldon; (USNM).

DIAGNOSIS.—Males of this species are distinguished from those of *C. mono* and *C. shepardi* by having a narrow tergal knob on segment 7 that is unsplit or slightly split at the tip. The males of *C. hornigi* are separated from those of *C. barberi* by the more slender epiproct (Fig. 64) and from *C. yosemite* by the appressed horns and the epiproct not being compoundly curved as in *C. yosemite*. The females of this species are not readily separated from others in the group but are a member of the subgroup that has the heavily sclerotized portion of the subgenital plate originating on the distal third of sternum 7. The lateral margins of the female plate converge distally, a character they share with the females of *C. yosemite*.

DISTRIBUTION.—CALIFORNIA: Mono Co.; NEVADA: Esmeralda Co.; (58). 10 February–4 March.

Capnia mono Nelson & Baumann

Figs. 93–96, 232, map Fig. 260

Capnia mono Nelson & Baumann 1987c: 493.

HOLOTYPE.—Male (and female allotype), California, Mono Co., 2 miles north of Topaz, Slinkard Creek, 5 November 1983, William D. Shepard, reared from nymphs; (USNM).

DIAGNOSIS.—This species is identified by the large, divided tergal knob on segment 7. The other member of the group having a broad knob is *C. shepardi*, from which this species may be distinguished by the deep epiproct borne on a thick neck. The neck of *C. shepardi* is thinner and is recognized as compoundly curved. Additionally, the membranous portion of the epiproct of *C. shepardi* is darkly colored especially near the truncate apex. The membrane of *C. mono* is uniformly white with the apex forming a sharper point than that of *C. shepardi*.

The female has a square subgenital plate similar to and indistinguishable from that of the northern females of *C. barberi*. These two forms may be separated from all other females in the group except *C. palomar* by the shorter plate, which begins on sternum 8 and is separated from sternum 7 by a narrow band of membrane. The female of *C. palomar* has a narrow bridge joining sterna 7 and 8.

DISTRIBUTION.—CALIFORNIA: Mono Co.; (28). 5 November–5 April.

Capnia palomar Nelson & Baumann

Figs. 117–120, 237, map Fig. 259

Capnia palomar Nelson & Baumann 1987c: 498.

HOLOTYPE.—Male (and female allotype), California, San Diego Co., Palomar Mountain, Fry Creek Campground, Fry Creek, Road S–6, 18 January 1985, R. W. Baumann and C. R. Nelson; (USNM).

DIAGNOSIS.—This species is distinguished by the horns nearly reaching the apex of the epiproct. No other species in the group has the horns so near the tip. It is also separated from the similar species, *C. hornigi*, by the narrower dorsal membranous area on the epiproct. It can be diagnosed from *C. shepardi* by the less-developed, compound curve of the epiproct (Fig. 120) and the more pointed apex in dorsal view.

DISTRIBUTION.—CALIFORNIA: Riverside Co.; San Diego Co.; (13). 18–19 January.

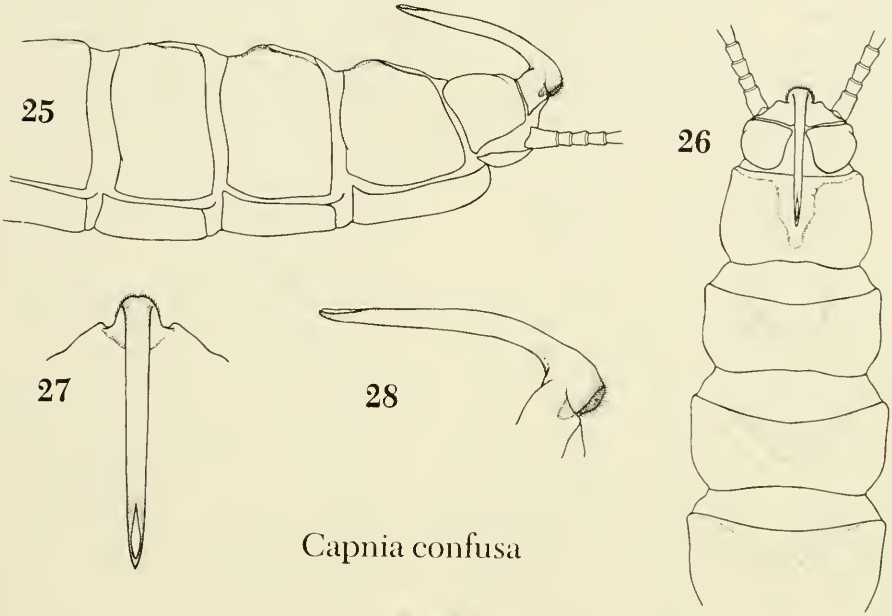
Capnia shepardi Nelson & Baumann

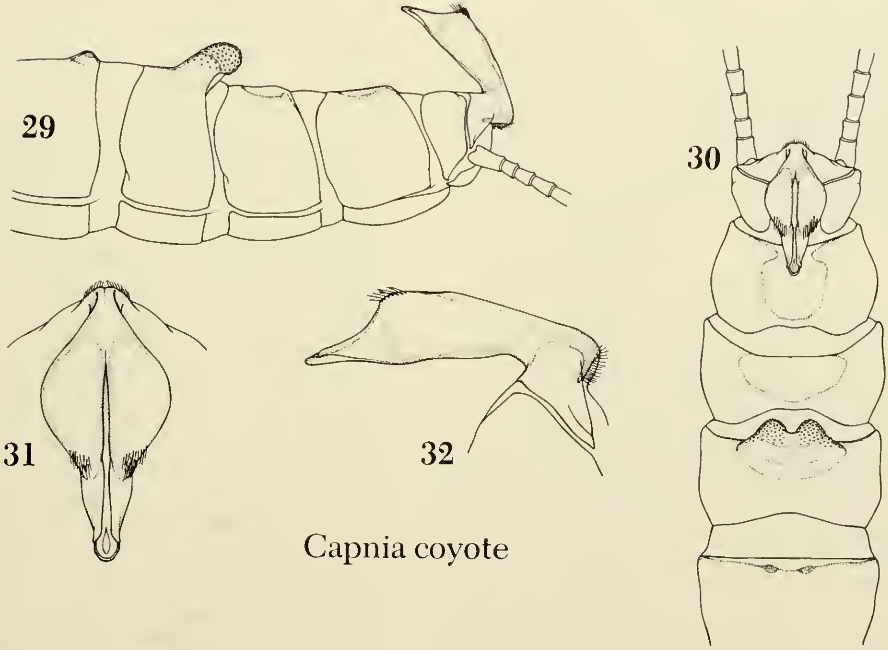
Figs. 157–160, 247, map Fig. 260

Capnia shepardi Nelson & Baumann 1987c: 495.

HOLOTYPE.—Male (and female allotype), California, Mono Co., Lee Vining Creek at Lee Vining Campground, 14 March 1985, R. W. Baumann and C. R. Nelson; (USNM).

DIAGNOSIS.—This species may be separated from other forms by the broad tergal knob on segment 7 and a compoundly curving epiproct. *Capnia mono* has a broad knob on tergum 7, but the epiproct does not curve compoundly. This species is the only member of the group with a truncate epiproctal tip and also the only member of the group with the





Figs. 25–28. *Capnia confusa* Claassen: 25, male terminalia, lateral; 26, male terminalia, dorsal; 27, male epiproct, dorsal; 28, male epiproct, lateral. Montana, Lincoln Co., Kootenai River, 28 March 1970, R. L. Newell.

Figs. 29–32. *Capnia coyote* Nelson & Baumann: 29, male terminalia, lateral; 30, male terminalia, dorsal; 31, male epiproct, dorsal; 32, male epiproct, lateral. California, Los Angeles Co., San Gabriel Mountains, Little Rock Creek, Cooper Canyon Campground, 31 March 1981, R. W. Baumann and J. A. Stanger.

membrane of the epiproct darkened. The females have distinctive notches in the subgenital plates marking the division of sterna 7 and 8. In *C. palomar* these notches are deeper, nearly dividing the segments.

DISTRIBUTION.—CALIFORNIA: Inyo Co.; Mariposa Co.; Mono Co.; Nevada Co.; Placer Co.; (73). 21 February–21 April.

Capnia yosemite Nelson & Baumann

Figs. 201–204, 257, map Fig. 259

Capnia yosemite Nelson & Baumann 1987c: 491.

HOLOTYPE.—Male (and female allotype), California, Mariposa Co., Big Creek, Highway 41, Summerdale Campground above Fish Camp, 18 March 1985, R. W. Baumann and C. R. Nelson; (USNM).

DIAGNOSIS.—The narrow, split knob on tergum 7, the extremely recurved epiproct, and the deep, broad area enclosed by the junction of the horns and the remainder of the epiproct differentiate this species from related forms. The female may be separated from others in the group by the strongly bulging subgenital plate (lateral view) that resembles a hemisphere. No other females have a subgenital plate that bulges to this extent. The lateral margins of the rectangular plate lack any notches such as those found in *C. shepardi* and *C. palomar*.

DISTRIBUTION.—CALIFORNIA: Mariposa Co.; Tuolumne Co.; (168). 18 March.

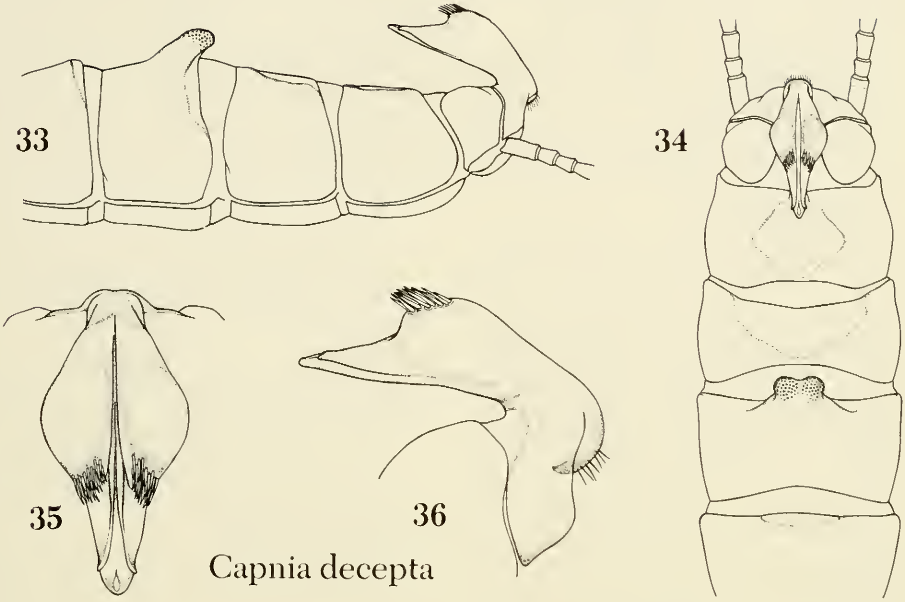
Californica Group

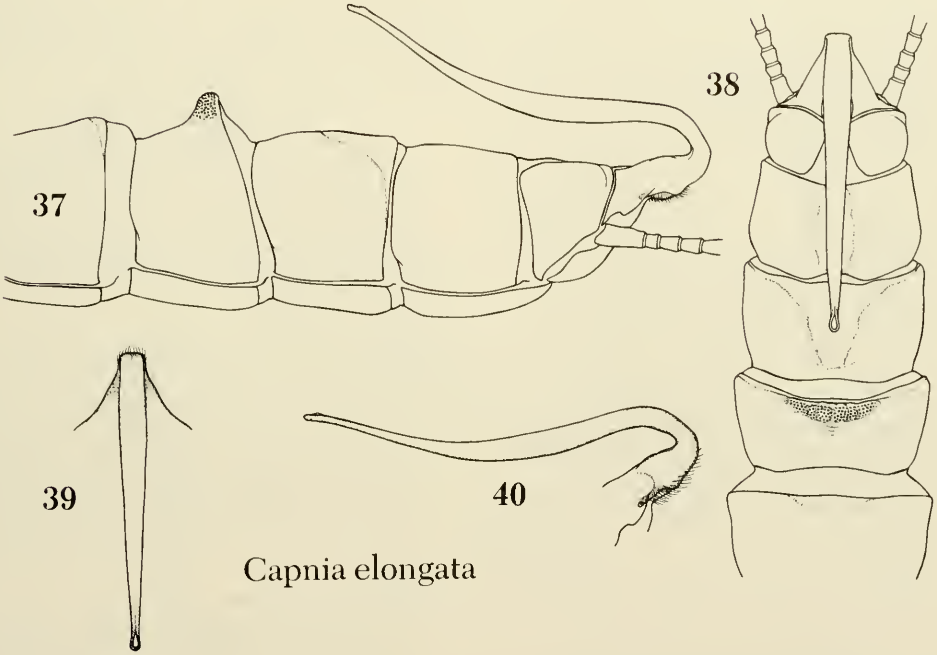
Members of the *Capnia californica* group include: *C. californica* Claassen, *C. jewetti* Frison, *C. ophiona* Nelson & Baumann, *C. quadrituberosa* Hitchcock, *C. regilla* Nelson & Baumann, *C. saratoga* Nelson & Baumann, *C. umpqua* Frison, and *C. ventura* Nelson & Baumann. Claassen (1924) described the male of *C. californica* from material collected in Cazadero (Sonoma Co.), California, by E. P. Van Duzee. A female collected from a small creek near Saratoga (Santa Clara Co.) was described by Jewett (1954a) as being that of *C. californica*. This female was collected with several males that are similar and closely related to *C. californica* but are morphologically distinct, which Nelson and Baumann (1987c) named *C. saratoga*. Several collections of *C. californica* containing series of males and females have been made in the Shasta-Trinity area of northern California. Two vials of specimens collected by D. G. Denning at Point Reyes National Seashore, near the type locality of *C. californica*, contain male and female specimens of *C. regilla* along with a single male of *C. californica*. This is the only record of sympatry among members of the group. Frison (1942) described *C. jewetti* from material collected in Muddy Creek, near Corvallis, Oregon. This species is placed in this group on the basis of the anteapical dorsal membranous area of the epiproct of the male and the sclerotized bar along the hind margin of the female subgenital plate (not emphasized in Frison's figure of the female), with the knobs on terga 5 and 6 interpreted as being autapomorphic. Frison (1942) also named and described *C. umpqua* and presented figures for both the male and the female. *Capnia quadrituberosa* was described from the male by Hitchcock (1958). Nelson and Baumann (1987c) also described *C. ophiona* and *C. ventura*.

The *californica* group is distinguished from other members of the genus by the following characters: male having an epiproct with an anteapical dorsal membranous area and having paired protuberances (knobs) on either tergum 8, 9, or both (exception *C. jewetti*, which has the paired knobs on terga 5 and 6). Females have a light-colored but sclerotized hind margin on the subgenital plate.

The group can be divided into two subgroups based on female characters (presence or absence of angular process projecting posteriorly over hind margin of subgenital plate) or three subgroups based on configurations of the male epiproct, including one subgroup with a pair of tergal knobs present on both terga 8 and 9; a subgroup with a single pair of knobs on tergum 9; and a third subgroup with tergal knobs on segments 5 and 6. Females are inseparable to species in the absence of males; hypotheses based on distribution may be useful in identifying females caught in the absence of males.

DISTRIBUTION.—This group is unique in having several morphologically distinct species located in close geographical proximity to each other. One species (*C. californica*) has its range separated by long distances. The group ranges from the Portland, Oregon, area south to Ventura County, California, with a disjunct species ranging in central and southern Arizona and northern Mexico. Several subdivisions of this general range are





Figs. 33–36. *Capnia decepta* (Banks): 33, male terminalia, lateral; 34, male terminalia, dorsal; 35, male epiproct, dorsal; 36, male epiproct, lateral. Arizona, Coconino Co., Oak Creek at Cave Springs Crossing, 27 December 1983, M. W. Sanderson, A82–20.

Figs. 37–40. *Capnia elongata* Claassen: 37, male terminalia, lateral; 38, male terminalia, dorsal; 39, male epiproct, dorsal; 40, male epiproct, lateral. California, Placer Co., North Fork American River near Colfax, 21 February 1985, R. W. Baumann and C. R. Nelson.

supported by species clusters, suggesting the occurrence of barriers that have contributed to speciation events in isolated areas.

Key to the Males of the Californica Group

1. Pairs of knobs present on both terga 8 and 9 (Figs. 10, 14, 110, 134) 2

— Pair of knobs present on tergum 9 only (Figs. 138, 142, 178, 190; weak on tergum 9 of *jewetti* but additional pairs of knobs present on terga 5 and 6 of *jewetti*, Fig. 70) 4

2(1). Upper process of epiproct absent (Fig. 112); dorsal membranous area of epiproct nearly reaching tip in dorsal view (Fig. 111) .... *ophiona* Nelson & Baumann

— Upper process present; represented by a narrow or blunt projection near anterior margin of dorsal membranous area (Figs. 12, 16, 136) 3

3(2). Upper process blunt (Fig. 136); declivity between upper and lower processes vertical or convex .... *quadrituberosa* Hitchcock

— Upper process narrow; declivity between upper and lower processes concave (Figs. 12, 16) .... *californica* Claassen

4(1). Upper process of epiproct present (Figs. 140, 144, 192) 5

— Upper process of epiproct absent (Figs. 72, 180) 7

5(4). Lower process of epiproct split at tip (Fig. 139); center of dorsal membranous area of epiproct nearer tip than midpoint between base of epiproct and tip of lower process; upper and lower processes of epiproct short .... *regilla* Nelson & Baumann

— Lower process of epiproct undivided at tip (Figs. 143, 191); dorsal membranous area of epiproct centered nearer midpoint between base and tip; lower process longer than upper .. 6

6(5). Upper process long; lower process longer, with lower surface forming a nearly straight line from base to near tip (Fig. 192) .... *ventura* Nelson & Baumann

— Upper process short, reduced to a small knob near anterior margin of membranous area; lower process shorter, lower surface curving upward on distal third (Fig. 144) .... *saratoga* Nelson & Baumann

7(4). Terga 5 and 6 each bearing paired knobs (Figs. 69, 70) .... *jewetti* Frison

— Terga 5 and 6 without paired knobs (Figs. 177, 178) .... *umpqua* Frison

Capnia californica Claassen

Figs. 9–16, 212–213, map Figs. 261, 273

Capnia californica Claassen 1924: 57, 1940: 92. Needham and Claassen 1925: 262. Hanson 1946: 238. Jewett 1954a: 175, 1956: 170, 1960: 144. Illies 1966: 134. Stark et al. 1986: 385.

Holotype.—Male, California, Sonoma Co., Cazadero, 14 April 1918, E. P. Van Duzee; (CAS).

Diagnosis.—The paired knobs present on both terga 8 and 9 and the split lower process on the tip of the epiproct distinguish this species from five species in the group. It may be further separated from the remaining species in the group on the basis of the combination of the following characters: the male epiproct of this species has two distinct processes on the tip region that have a concave area between them. *Capnia quadrituberosa* has a remnant of an upper process; however, the declivity below this remnant falls abruptly to the lower process without a hint of concavity. The upper process of the epiproct is absent in *C. ophiona*.

Distribution.—Arizona: Cochise Co.; Gila Co.; Graham Co.; Pima Co.; Santa Cruz Co. California: Lake Co.; Napa Co.; Plumas Co.; Shasta Co.; Sonoma Co.; Trinity Co. Chihuahua: Sierra Madre Occidental; (63). 10 January–27 April.

Additional females of uncertain species, but members of this group, are: California: Santa Clara Co., 3.5 road miles east of summit of Mt. Hamilton, I-26-1974, J. Powell; San Benito Co., 5 miles west of Paicines Lime Kiln Rd., III-24-66, R. D. Usinger.

Capnia jewetti Frison

Figs. 69–72, 226, map Fig. 263

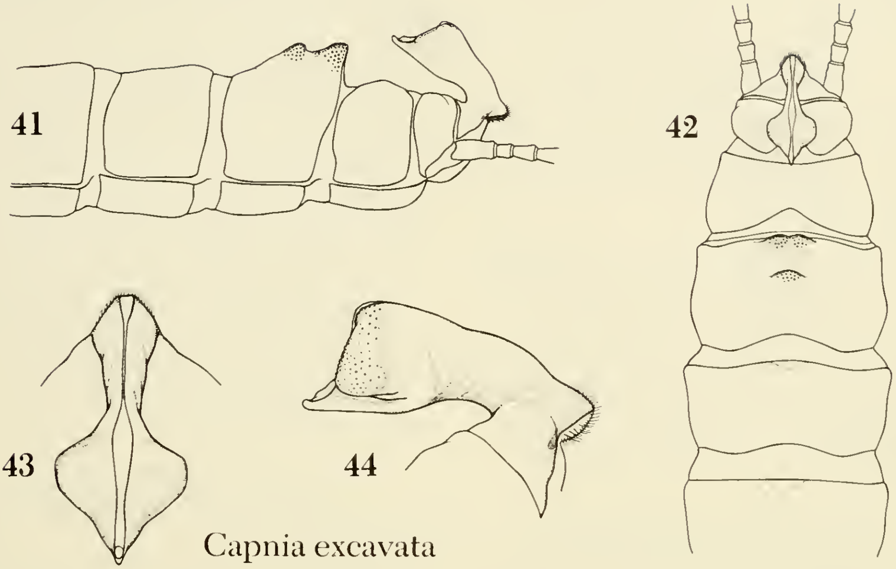
Capnia jewetti Frison 1942: 63. Hanson 1946: 239. Jewett 1959: 46. Illies 1966: 139. Stark et al. 1986: 385.

Holotype.—Male (and female allotype), Oregon, Benton Co., 14 miles south of Corvallis, Muddy Creek, 10 February 1938, S. G. Jewett, Jr.; (CAS).

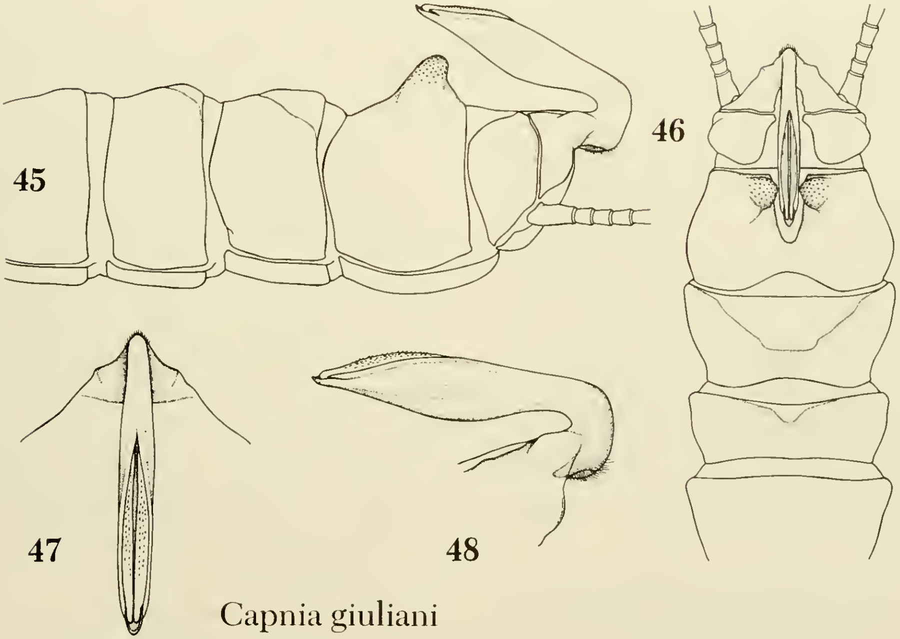
Diagnosis.—The male of this species is easily separated from other members of the group on the basis of the paired knobs present on terga 5 and 6 and the absence of tergal knobs on 8 and 9. Because of similarities of the shape of the epiproct and the placement of the dorsal membranous area on the epiproct, this species is most closely related to *C. umpqua*.

The female of *C. jewetti* is similar to that of *C. umpqua* and other members of the group in that it lacks a medial flap overhanging the sclerotized hind margin of the subgenital plate. Insufficient characters are available to distinguish females in the group as a whole, except to divide them into two complexes based on the subgenital flap.

Distribution.—Oregon: Benton Co.; Clackamas Co.; Clatsop Co.; Columbia Co.;



Figs. 41–44. *Capnia excavata* Claassen: 41, male terminalia, lateral; 42, male terminalia, dorsal; 43, male epiproct, dorsal; 44, male epiproct, lateral. California, Plumas Co., Mosquito Creek at junction North Fork Feather River, 14 February 1985, R. W. Baumann and C. R. Nelson.



Figs. 45–48. *Capnia giulianii* Nelson & Baumann: 45, male terminalia, lateral; 46, male terminalia, dorsal; 47, male epiproct, dorsal; 48, male epiproct, lateral. California, Inyo Co., Lone Pine Creek, Whitney Portal Campground, 3 April 1981, R. W. Baumann and J. A. Stanger.

Washington Co.; Yamhill Co. WASHINGTON: Clallam Co.; (42). 2 February–14 April.

Capnia ophiona Nelson & Baumann

Figs. 109–112, map Fig. 273

Capnia ophiona Nelson & Baumann 1987c: 506.

HOLOTYPE.—California, Butte Co., Butte Creek, Butte Meadows Campground, 15 February 1985, R. W. Baumann and C. R. Nelson; (USNM).

DIAGNOSIS.—This species is distinguished from both *C. californica* and the closely related *C. quadrituberosa* by the lack of an upper process on the epiproct and the absence of a sclerotized bridge separating the dorsal membranous area from the anterior margin of the epiproct. The female is unknown.

DISTRIBUTION.—CALIFORNIA: Butte Co.; (1). 15 February.

Capnia quadrituberosa Hitchcock

Figs. 133–136, 241, map Fig. 273

Capnia quadrituberosa Hitchcock 1958: 77. Jewett 1960: 146. Illies 1966: 146. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), California, Butte Co., small stream tributary to Feather River crossing Route 40A north of Oroville, 22 January 1955; (USNM).

DIAGNOSIS.—The male of this species most closely resembles that of *C. californica*. It may be separated from this species by its reduced upper process, the anterior margin of which drops perpendicularly until reaching the lower process which extends forward. It is also separated from *C. ophiona* by this perpendicular front margin on the epiproct; the epiproct of *C. ophiona* slopes directly from the dorsal membranous area to the lower process, the upper process being absent.

DISTRIBUTION.—CALIFORNIA: Butte Co.; Contra Costa Co.; El Dorado Co.; Nevada Co.; Placer Co.; Sacramento Co.; Tuolumne Co.; (204). 22 January–18 May.

Capnia regilla Nelson & Baumann

Figs. 137–140, 242, map Fig. 262

Capnia regilla Nelson & Baumann 1987c: 508.

HOLOTYPE.—Male (and female allotype), California, Marin Co., Point Reyes National Seashore, Bear Valley Creek, 25 May 1975, D. G. Denning; (USNM).

DIAGNOSIS.—This species is distinguished from other members of the group by features of the male epiproct and tergal knobs and the subgenital plate of the female. *Capnia regilla* is distinguished from *C. californica*, *C. ophiona*, and *C. quadrituberosa* by its lacking tergal knobs on segment 8. It is further separated from members of these species by the presence of a two-lobed upper process of the male epiproct and the inflated region below the lower process. *Capnia regilla* may be separated from *C. ventura* and *C. saratoga* by the bifid tip of the lower process and the single-lobed upper process of the epiproct. The female of *C. regilla* is closely allied to the above species as judged by the presence of the medial angular flap on the subgenital plate. Characters for separating the females within this subgroup are lacking at this time.

DISTRIBUTION.—CALIFORNIA: Marin Co.; (27). 14 March–25 May.

Capnia saratoga Nelson & Baumann

Figs. 141–144, 243, map Fig. 262

Capnia saratoga Nelson & Baumann 1987c: 505.

HOLOTYPE.—Male (and female allotype), California, Santa Clara Co., small creek near Saratoga, 25 February 1940, S. G. Jewett, Jr.; (USNM).

DIAGNOSIS.—This species is distinguished from *C. californica*, *C. ophiona*, and *C. quadrituberosa* by the undivided tip of the lower process of the epiproct and the presence of a single pair of tergal knobs. It is separated from *C. umpqua* and *C. jewetti* on the basis of the wide area between the dorsomedial membranous area of the epiproct and the tip of the lower process. The extremely shortened upper process in this species separates it from the males of *C. regilla* and *C. ventura*. The male is further distinguished from that of *C. ventura* by the upcurving lower margin of the epiproct (Fig. 144). The female of this species belongs to the group of species having an overhanging angular appendage on the subgenital plate (Fig. 243).

DISTRIBUTION.—CALIFORNIA: Santa Clara Co.; (4). 25 February.

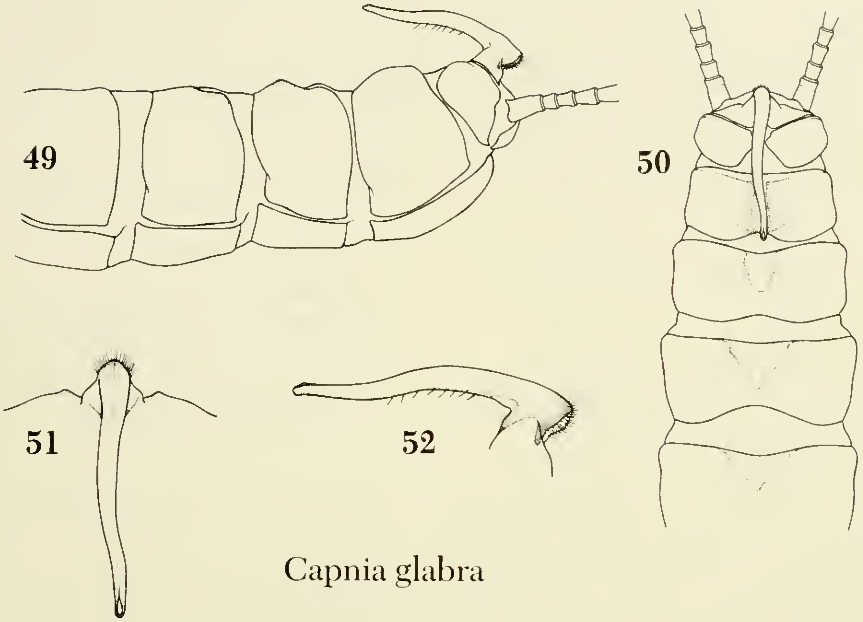
Capnia umpqua Frison

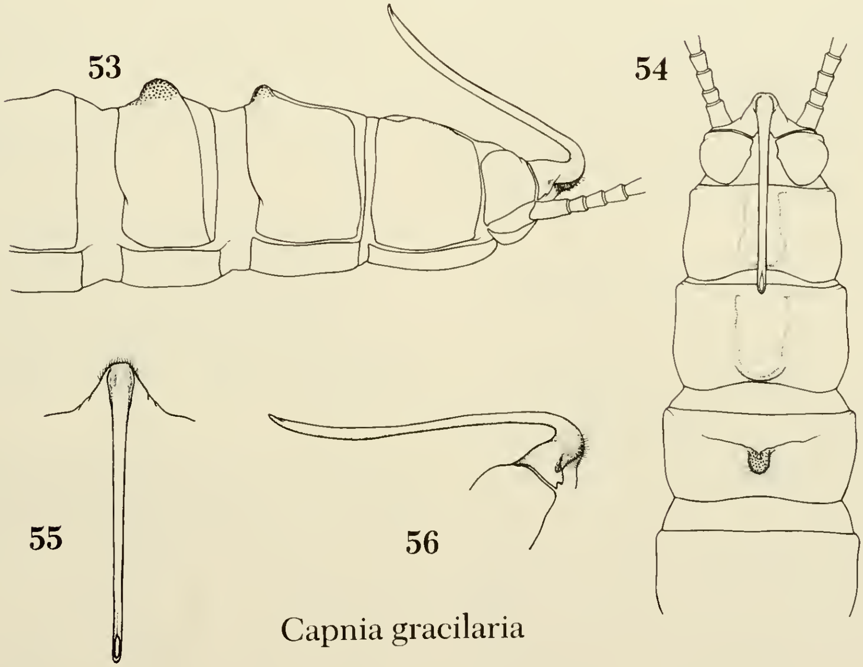
Figs. 177–180, 252, map Fig. 263

Capnia umpqua Frison 1942: 65. Hanson 1946: 239. Jewett 1959: 48, 1960: 146. Illies 1966: 148. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), Oregon, Douglas Co., Umpqua River, 21 February 1939, S. G. Jewett, Jr.; (INHS).

DIAGNOSIS.—This species is most closely related to *C. jewetti*, from which it may be





Figs. 49–52. *Capnia glabra* Claassen: 49, male terminalia, lateral; 50, male terminalia, dorsal; 51, male epiproct, dorsal; 52, male epiproct, lateral. California, Placer Co., Ward Creek, Hwy 89, near Lake Tahoe, 22 February 1985, R. W. Baumann and C. R. Nelson.

Figs. 53–56. *Capnia gracilaria* Claassen: 53, male terminalia, lateral; 54, male terminalia, dorsal; 55, male epiproct, dorsal; 56, male epiproct, lateral. Montana, Missoula Co., Rattlesnake Creek above Greenough Park, Missoula, 17 March 1969, R. W. Baumann.

separated by the absence of paired tergal knobs on segments 5 and 6. *Capnia umpqua* has paired knobs only on segment 9. The females of the two species are similar and their ranges overlap in the Willamette basin.

Distribution.—California: Alameda Co.; Contra Costa Co.; Humboldt Co.; Marin Co.; Mendocino Co.; Monterey Co.; Orange Co.; Santa Clara Co.; Shasta Co.; Sonoma Co.; Stanislaus Co.; Trinity Co. Oregon: Curry Co.; Douglas Co.; Josephine Co.; Linn Co.; Marion Co.; Polk Co.; (518). 25 January–2 April.

Capnia ventura Nelson & Baumann

Figs. 189–192, 255, map Fig. 262

Capnia ventura Nelson & Baumann 1987c: 503.

Holotype.—Male (and female allotype), California, Ventura Co., Wheeler Gorge Campground, North Fork Matilija Creek, 23 January 1985, R. W. Baumann and C. R. Nelson; (USNM).

Diagnosis.—*Capnia ventura* is distinguished from *C. californica*, *C. ophiona*, and *C. quadrituberosa* by having a single pair of tergal knobs and a well-developed upper process. It is separated from the closely related *C. saratoga* (Fig. 144) by the longer upper process of the male epiproct (Fig. 192) and from *C. regilla* (Fig. 140) by the longer lower process. All three of these closely related species are allopatric.

Distribution.—California: Santa Barbara Co.; Ventura Co.; (73). 23–24 January.

Coloradensis Group

The members of this small group are united on the basis of a synapomorphic downward bending of the tip of the male epiproct. They were probably derived from an ancestor of the *decepta* group. The three members of the group are *C. coloradensis* Claassen, *C. hitchcocki* Nelson & Baumann, and *C. petila* Jewett. The group status of this assemblage is somewhat tenuous because of the variable location of the tergal knob. The overall shape of the epiproct, including the drooping tip and straight shaft, along with the similarities of the darkened plates of the females, however, are interpreted as being apomorphic, indicating that a monophyletic relationship may exist.

Distribution.—Members of the group live in streams of the central and southern Rocky Mountains and as an apparently isolated population south of San Francisco Bay. All three species tend to emerge later, in March and April. This characteristic late emergence is unusual because of their occurrence at low elevations where they could be expected to emerge earlier in the year.

Key to the Males of the Coloradensis Group

1. Tergal knob on segment 7 (Fig. 121) .... *petila* Jewett

— Tergal knob on segment 8 2

2(1). Tergal knob strongly tuberculate; epiproct widening slightly toward tip in lateral view (Fig. 21) .... *coloradensis* Claassen

— Tergal knob weakly differentiated; epiproct narrowing toward tip or of uniform width throughout length in lateral view (Fig. 60) .... *hitchcocki* Nelson & Baumann

Key to the Females of the Coloradensis Group

1. Subgenital plate much darker than surrounding sclerites (Figs. 215, 223) 2

— Subgenital plate evident, but not much darker than surrounding sclerites (Fig. 238) .... *petila*

2(1). Subgenital plate trapezoidal, with short, parallel side forming posterior margin, sides of plate notched near posterior margin (Fig. 223) .... *hitchcocki*

— Subgenital plate not trapezoidal, posterior margin rounded, lateral notches lacking (Fig. 215) .... *coloradensis*

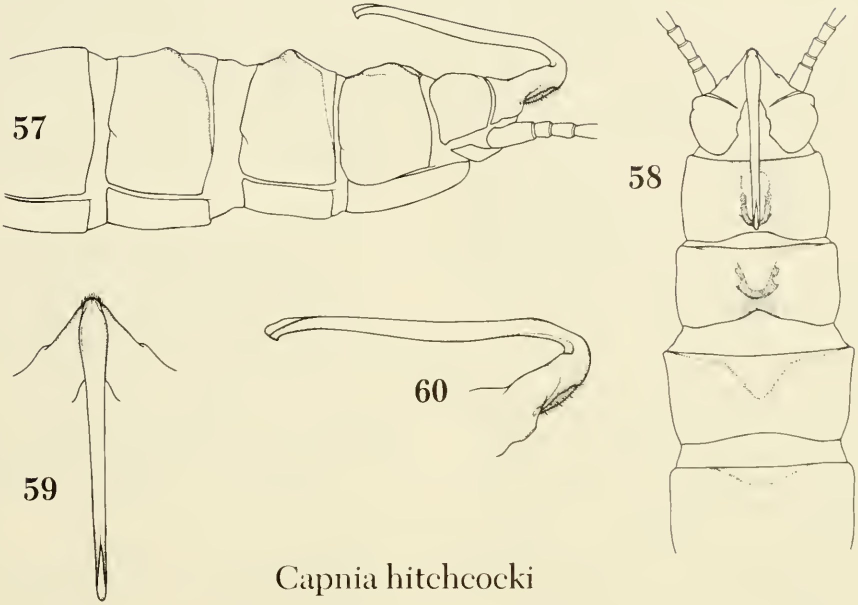
Capnia coloradensis Claassen

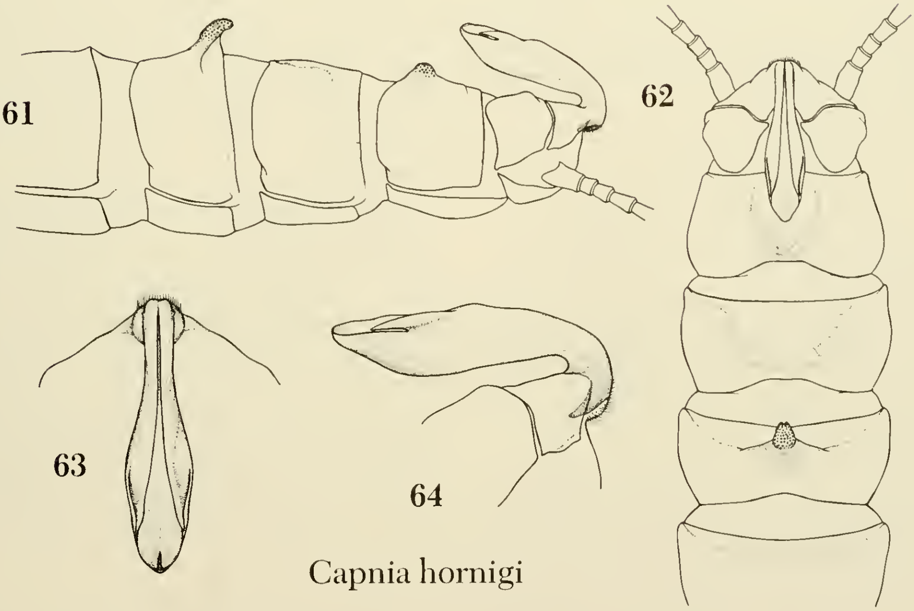
Figs. 21–24, 215, map Fig. 264

Capnia coloradensis Claassen 1937: 79, 1940: 92. Hanson 1946: 238. Gaufin 1964a: 223. Ricker 1965: 487. Gaufin et al. 1966: 48. Illies 1966: 134. Knight and Gaufin 1966: 669, 1967: 348. Nebeker and Gaufin 1966: 38, 1967a: 419, 1968: 2. Logan and Smith 1966: 1. Baumann et al. 1977: 66. Stark et al. 1986: 385.

Holotype.—Male (and female allotype), Colorado, El Paso Co., Seven Falls, N Cheyenne Canyon, 3 August 1921; (CU).

Diagnosis.—The male of this species may be distinguished from any other in the genus by its having a tubelike epiproct, with the extreme tip dropping downward as a blunt extension, and a prominent tergal knob on segment 8. The female has a subgenital plate similar to that of some members of the *decepta* group, a dark, heavily sclerotized plate which has several lighter lines running longitudinally. The female has a darker plate than the other members of the group. Ricker (1965) was correct in redescribing the female of this species; the female drawing given by Claassen





Figs. 57–60. *Capnia hitchcocki* Nelson and Baumann: 57, male terminalia, lateral; 58, male terminalia, dorsal; 59, male epiproct, dorsal; 60, male epiproct, lateral. California, Alameda/Santa Clara County line, Arroyo Mocho Creek, 20 miles south of Livermore, San Antonio Valley Road, 19 March 1985, R. W. Baumann and C. R. Nelson.

Figs. 61–64. *Capnia hornigi* Baumann & Sheldon: 61, male terminalia, lateral; 62, male terminalia, dorsal; 63, male epiproct, dorsal; 64, male epiproct, lateral. Nevada, Esmeralda Co., White Mountains, Middle Creek, 10 February 1977, A. L. Sheldon.

(1937) appears to be *Utacapnia logana* (Nebeker & Gaufin). The record of *C. decepta* (Banks 1907b, as *Arsapnia decepta*) from Alberta is most probably a female of this species.

DISTRIBUTION.—ALASKA: Anchorage, 10 miles southeast; Kantishna Hills, Denali National Park. ALBERTA: Athabasca River, Jasper National Park, 4,180 feet; Lobstick River at Highway 16. BRITISH COLUMBIA: Kelsall Lake area; Meadow Creek, Highway 3; Manning Provincial Park, Similkameen River; Mosquito Flats, Chilkat Pass; Moyie River above lake; Shingle Creek; Tesla River, Stone Mountain Provincial Park. COLORADO: El Paso Co.; Grand Co.; Gunnison Co.; Hinsdale Co.; Jackson Co.; Lake Co.; Larimer Co.; Mineral Co.; Routt Co.; San Juan Co. IDAHO: Adams Co.; Benewah Co.; Blaine Co.; Boise Co.; Bonner Co.; Cassia Co.; Clearwater Co.; Custer Co.; Fremont Co.; Idaho Co.; Latah Co.; Shoshone Co.; Teton Co.; Valley Co. MONTANA: Broadwater Co.; Gallatin Co.; Lincoln Co.; Meagher Co.; Ravalli Co. NEW MEXICO: Taos Co. UTAH: Box Elder Co. WYOMING: Albany Co.; Lincoln Co.; Park Co.; Sublette Co.; Teton Co. YUKON TERRITORY: Kluane, Boutellier Creek; Christmas Creek; North Fork Pass, Ogilvie Mountains; (747). 29 January–July.

Capnia hitchcocki Nelson & Baumann

Figs. 57–60, 223, map Fig. 265

Capnia lineata Hitchcock 1958: 80. Jewett, 1960: 145.
Capnia hitchcocki Nelson & Baumann 1987c: 512.

HOLOTYPE.—Male (and female allotype), California, Alameda/Santa Clara County line, Arroyo Mocho Creek, 20 miles south of Livermore, San Antonio Valley Road, 19 March 1985, R. W. Baumann and C. R. Nelson; (USNM).

DIAGNOSIS.—The epiproct of this species is very similar to that of *C. petila*, although the latter species is much smaller. The two species are distinguished on the basis of the tergal knob, which is on segment 7 in *C. petila* and on segment 8 of *C. hitchcocki*. The heavily colored subgenital plate of the female is dissimilar from any other winter stoneflies that would be collected in the streams of this region. The dark brown, notched plate might be confused with that of members of the Barberi group, but in that group the plate is black, the color of which seems to be external. The dark brown color of the female of *C. hitchcocki* is internal, overlain by lighter sclerotization. This species was originally collected in the 1950s and identified as *C. lineata*. The smaller size, the presence of a diminutive tergal knob, and the dark female plate differentiate this species from *C. lineata*.

DISTRIBUTION.—CALIFORNIA: Alameda Co.; Santa Clara Co.; Stanislaus Co.; (27). 19 March.

Capnia petila Jewett

Figs. 121–124, 238, map Fig. 265

Capnia petila Jewett 1954b: 546, 1959: 47. Illies 1966: 145. Nebeker and Gaufin 1967a: 238, 1967b: 418, 1968: 3. Newell 1970: 50. Zwick 1973: 376. Baumann et al. 1977: 73. Stark et al. 1986: 385.

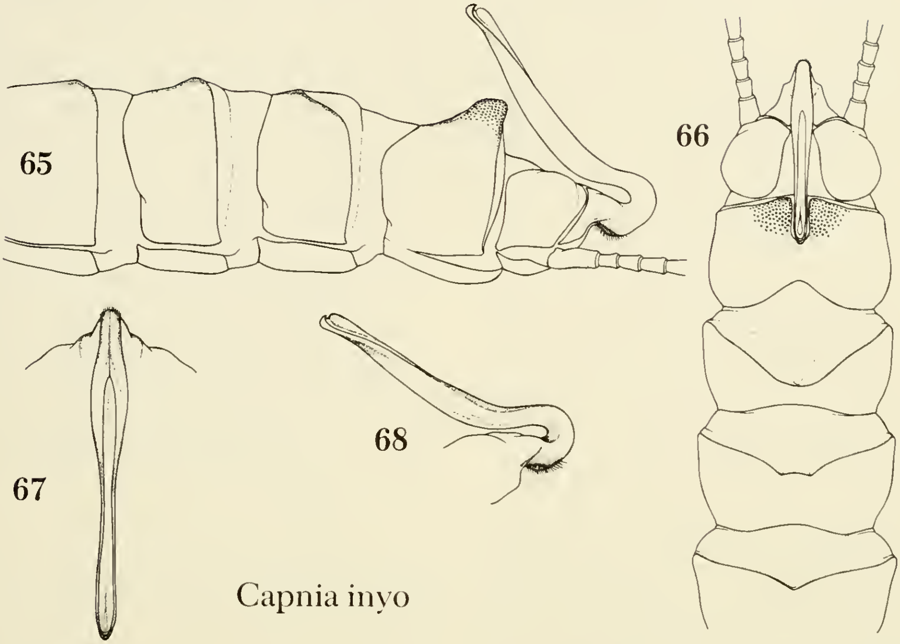
HOLOTYPE.—Male, Oregon, Baker Co., Spring Creek, tributary of Powder River, 30 March 1952, J. H. Baker; (CAS). Female allotype, Montana, Ravalli Co., Big Creek; (USNM).

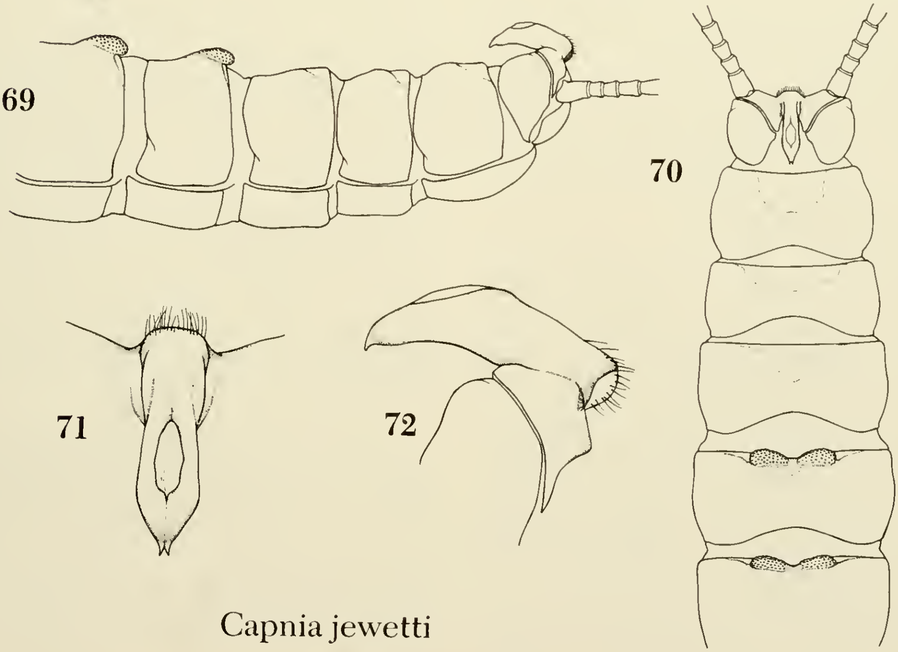
DIAGNOSIS.—The male of this species resembles a small *C. coloradensis*, from which it is easily distinguished by the presence of the tergal knob on abdominal segment 7 in *C. petila* and on segment 8 in *C. coloradensis*. The subgenital plates of these two species are similar in shape, but that of *C. coloradensis* is much darker and more well defined (Fig. 238).

DISTRIBUTION.—ALASKA: Caribou Creek, Utiladuct; Talkeetna, Fern Mine Road; Monument Creek tributary of Chena River; West Fork Chena River. ALBERTA: Banff National Park. BRITISH COLUMBIA: Lytton, Botanie Lake; Manning Provincial Park, Similkameen River. IDAHO: Boise Co.; Bonneville Co.; Custer Co.; Idaho Co. MONTANA: Broadwater Co.; Cascade Co.; Flathead Co.; Gallatin Co.; Glacier Co.; Lake Co.; Missoula Co.; Ravalli Co. OREGON: Baker Co. UTAH: Box Elder Co. WYOMING: Park Co.; Sublette Co. YUKON TERRITORY: Kluane, Boutellier Creek; (267). 7 March–16 August.

Decepta Group

The *C. decepta* group forms a cluster of closely related species. The species included in this group are: *C. arapahoe* Nelson & Kondratieff, *C. coyote* Nelson & Baumann, *C. decepta* (Banks), *C. pileata* Jewett, *C. teresa* Claassen, *C. sequoia* Nelson & Baumann, *C. tumida* Claassen, and *C. utahensis* Gaufin & Jewett.





Figs. 65–68. *Capnia inyo* Nelson & Baumann: 65, male terminalia, lateral; 66, male terminalia, dorsal; 67, male epiproct, dorsal; 68, male epiproct, lateral. California, Inyo Co., Independence Creek, Grays Meadow Campground, 25 January 1985, R. W. Baumann and C. R. Nelson.

Figs. 69–72. *Capnia jewetti* Frison: 69, male terminalia, lateral; 70, male terminalia, dorsal; 71, male epiproct, dorsal; 72, male epiproct, lateral. Oregon, Benton Co., Muddy Creek, 17 February 1985, G. R. Fiala.

Arsapnia decepta was described by Banks from Fort Collins, Colorado, in 1897 in a new genus. Claassen (1924) placed *Arsapnia* in synonymy with *Capnia* Pictet after a careful study of Pictet's description and figures of the European type-species, *C. nigra*. Claassen (1924) described the males of *C. tumida* and *C. teresa* based on California material. The female of *C. tumida* was described by Frison (1942), who included figures of the male based on material from Portland, Oregon. Later Jewett (1966) described *C. pileata* from specimens taken at the same locality from which Frison described the female of *C. tumida*. *Capnia pileata* Jewett was named from the description of the female given by Frison (1942), the figures of both male and female given by Frison (1942), and the diagnosis given in Jewett (1966). Jewett (1966) also described a female allotype for *C. tumida* and presented figures of both the male and the female of this species. Another species belonging to this group, *C. barbata* Frison (1944), was named from material from Longmount (correct spelling is Longmont), Colorado. The differences between this species and *C. decepta* fall within the range of variability found in series of *C. decepta*. Additionally, the type localities of *C. barbata* and *C. decepta* are less than 25 miles apart. We place *C. barbata* in synonymy under *C. decepta*, which has priority.

The following combination of characters distinguishes the *decepta* group from other members of the genus: a large, expanded epiproct consisting of a neck, bulb, and tip, the parts differentiated from each other by degree of gibbosity (Figs. 209, 210); a dorsal tubercle on tergum 7 of the male abdomen that is produced posteriorly into a knob covered with several types of sensillae and which is bifid to varying degrees; and a subgenital plate in the female that is darkly sclerotized and is approximately two-fifths the width of sternum 8. Both sexes are macropterous.

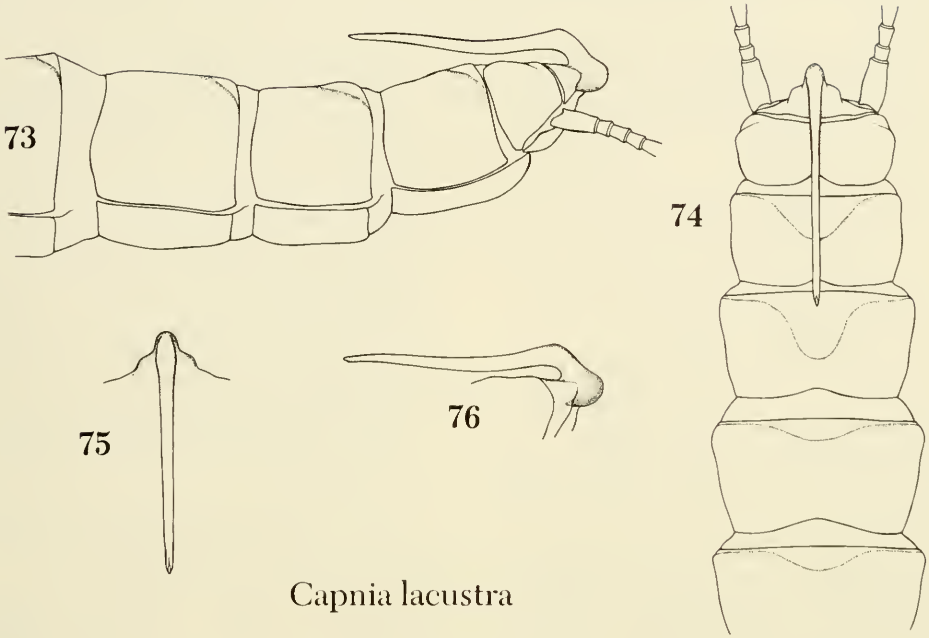
A knowledge of the following terms will facilitate identification when using the key to this group. These defined features are shown in Figures 209, 210. The epiproct is the recurved appendage of tergum 11 of the male which serves as an intromittent organ. The epiproct is divided into three regions including the neck, bulb, and tip. The neck serves as the basal attachment of the epiproct to the remainder of tergum 11. The bulb is the region distal to the neck and is inflated to varying degrees in different species of this group. The limits between the neck and bulb are somewhat arbitrary in some specimens but are generally distinct. The slope where the neck and bulb meet is the posterior declivity. The tip of the epiproct is the narrow, attenuated structure that joins the bulb at the anterior declivity. Dorsal bristles of several sizes are generally present on the leading edge of the dorsal margin of the anterior declivity. They are absent in specimens of *C. sequoia*. A specimen viewed from the dorsal aspect will show a median furrow that divides the tip and bulb in half on the upper surface. The extent of widening of this furrow has some taxonomic value in distinguishing species. The lower surface of the epiproct lacks any dividing furrows or sutures.

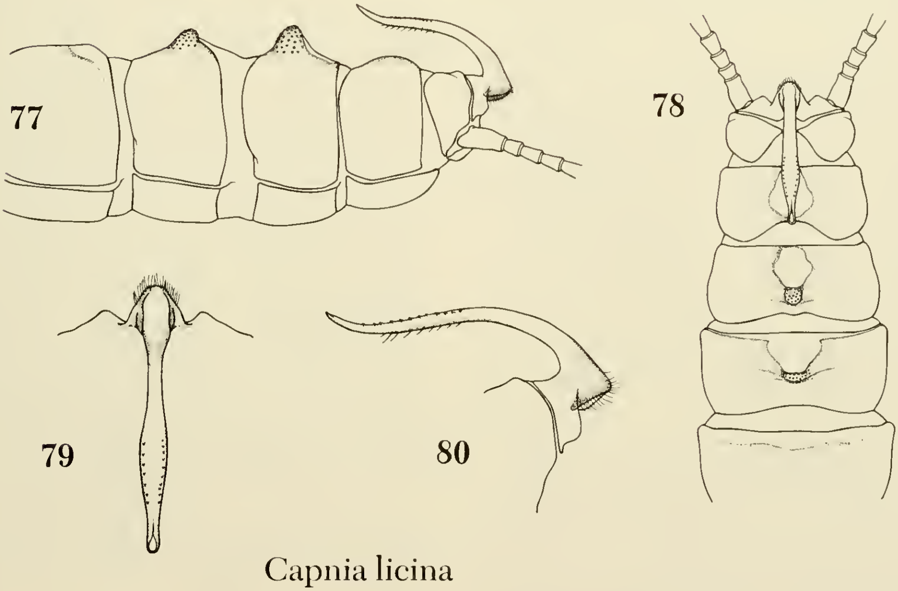
DISTRIBUTION.—The members of this group inhabit smaller streams in western North America from Vancouver Island south to coastal Oregon and then inland down the southern Cascade Mountains and Sierra Nevada to the ranges of mountains surrounding the Los Angeles basin. Other members of the group are then found south and eastward in Arizona, New Mexico, Colorado, and Mexico in streams that drain immediately from the bases of the Southern Rocky Mountains and the island mountains that dot the desert in those areas. These species apparently live in a transition zone between the mountains and the Great Plains on the eastern portion of their range. One unconfirmed record of *C. decepta* from Banff, Alberta, exists in the literature (Banks 1907b); this record is probably from a female of *C. coloradensis*.

This group is conspicuously absent from the main mass of the Rocky Mountains (except a record of a female of *C. decepta* from Steamboat Springs, Routt County, Colorado, reported by Needham and Claassen [1925], which could easily have been a mistaken determination of the female of *C. coloradensis* Claassen). This group is also absent from the Great Basin.

Key to the Males of the Decepta Group

1. Bulb of epiproct spherical; sides of posterior declivity bearing fine bristles; tip of epiproct narrow and short, approximately one-half the length of epiproctal bulb (Figs. 167, 168); mountains surrounding Los Angeles basin .... *teresa* Claassen





Figs. 73–76. *Capnia lacustra* Jewett: 73, male terminalia, lateral; 74, male terminalia, dorsal; 75, male epiproct, dorsal; 76, male epiproct, lateral. California, El Dorado Co., Lake Tahoe, Emerald Bay, depth 116–198 feet, 11 July 1962, T. C. Frantz and A. J. Cordone.

Figs. 77–80. *Capnia licina* Jewett: 77, male terminalia, lateral; 78, male terminalia, dorsal; 79, male epiproct, dorsal; 80, male epiproct, lateral. Washington, Whatcom Co., North Fork Nooksack River, 11 miles east of Glacier, 1,900 feet, 18 February 1966, K. E. Vander Mey.

— Bulb of epiproct not spherical; sides of posterior declivity lacking bristles although bristles may be present on upper surface of the neck of epiproct 2

2(1). Epiproct four or more times as long as deep in lateral view, lacking inflated bulb (Figs. 4, 184) . . 3

— Epiproct about three times as long as deep in lateral view, inflated epiproctal bulb present (Figs. 32, 36, 152, 172) 4

3(2). Tergum 7 bearing distinct knob (Fig. 1); epiproct about seven times as long as wide in dorsal view (Fig. 3), not widened basally . . . . *arapahoe* Nelson & Kondratieff

— Tergum 7 lacking a distinct knob (Fig. 181); epiproct about three times as long as wide, widened near base (Fig. 183) . . . . *utahensis* Gaufin & Jewett

4(2). Bulb tapering uniformly to meet base of tip gradually when viewed from above (Figs. 31, 35) 5

— Bulb ending abruptly distally, base of tip much narrower than width of distal edge of bulb (Figs. 127, 151, 171) 6

5(4). Bulb of epiproct inflated in lateral aspect, especially near anterior declivity; bases of spines on anterior declivity, not above a line drawn along upper margin of posterior declivity (Fig. 36); ratio of greatest length of gibbosity to greatest height of epiproct when measured in lateral view less than 1.9; mountains of Colorado, New Mexico, Mexico, Arizona, and southern Nevada . . . . *decepta* (Banks)

— Bulb of epiproct not greatly inflated in lateral aspect but gradually increasing in diameter from neck region and then slowly decreasing in diameter beginning at anterior declivity (Fig. 32); bases of some of the spines of anterior declivity above a line drawn along posterior declivity; epiproctal ratio greater than 2.0; San Bernardino and San Gabriel mountains of southern California . . . . *coyote* Nelson & Baumann

6(4). Anterior declivity concave (Figs. 127, 128); dorsal bristles on a transverse carina; bulb of epiproct with gibbosity concentrated nearer anterior declivity than neck; northwestern Oregon, northern California . . . . *pileata* Jewett

— Anterior declivity slightly convex (Figs. 152, 172); dorsal bristles in transverse row or clumped or absent, not on a heavy carina but on sloping junction of bulb and anterior declivity; bulb of epiproct with gibbosity extending from neck region to anterior declivity 7

7(6). Anterior declivity lacking bristles, sloping evenly from area of greatest gibbosity to apex, carina absent (Figs. 151, 152) . . . . *sequoia* Nelson & Baumann

— Anterior declivity with sparse bristles arranged in a row of small but distinct carina on top of anterior declivity (Figs. 171, 172) . . . *tumida* Claassen

Key to the Females of the Decepta Group (including *C. arapahoe* unknown)

1. Subgenital plate notched apically (Fig. 249) . . *teresa*

— Subgenital plate entire on posterior margin 2

2(1). Subgenital plate joined to sternum 7 (Fig. 239) . . . . *pileata*

— Subgenital plate separated from sternite 7 by intersegmental membrane 3

3(2). Subgenital plate as wide as or wider than long (may be wider at base narrowing to distal margin; subgenital plate 0.24–0.35 mm in length (Fig. 250) . . . . *tumida*

— Subgenital plate longer than wide; subgenital plate 0.40–0.54 mm in length. 4

4(3). Width of subgenital plate one-fourth or less width of sternum 8 (Fig. 253) . . . . *utahensis*

— Width of subgenital plate one-third or more width of sternum 8 5

5. Inhabiting streams of Mohave River drainage system in southern California (Fig. 217) . . . *coyote*

— Inhabiting streams in Spring Mountains, Nevada, Sierra San Pedro Martir, Baja California, and drainages south and east of the Colorado River (Fig. 218) . . . . *decepta*

Capnia arapahoe Nelson & Kondratieff

Figs. 1–4, map Fig. 268

Capnia arapahoe Nelson & Kondratieff 1988: 77.

HOLOTYPE.—Male, Colorado, Larimer Co., Elkhorn Creek at junction of Highway 14, 22 miles west of Fort Collins, 2,012 m (6,600′), 3 April 1987, B. C. Kondratieff and P. Zwick; (USNM).

DIAGNOSIS.—*Capnia arapahoe* is placed in the Decepta group based on the presence of a well-differentiated tergal knob on abdominal segment 7 and on the presence of horns on the tip of the epiproct. It differs from other members of the group in lacking a mesal bulbous expansion of the epiproct, and in the slim profile of the epiproct in both dorsal and lateral aspects. This species may be confused with *C. confusa* Claassen based on the general shape of the epiproct, but it can be distinguished from *C. confusa* by the presence of a tuberculate knob on tergum 7 and an epiproct that recurves slightly and bears horns.

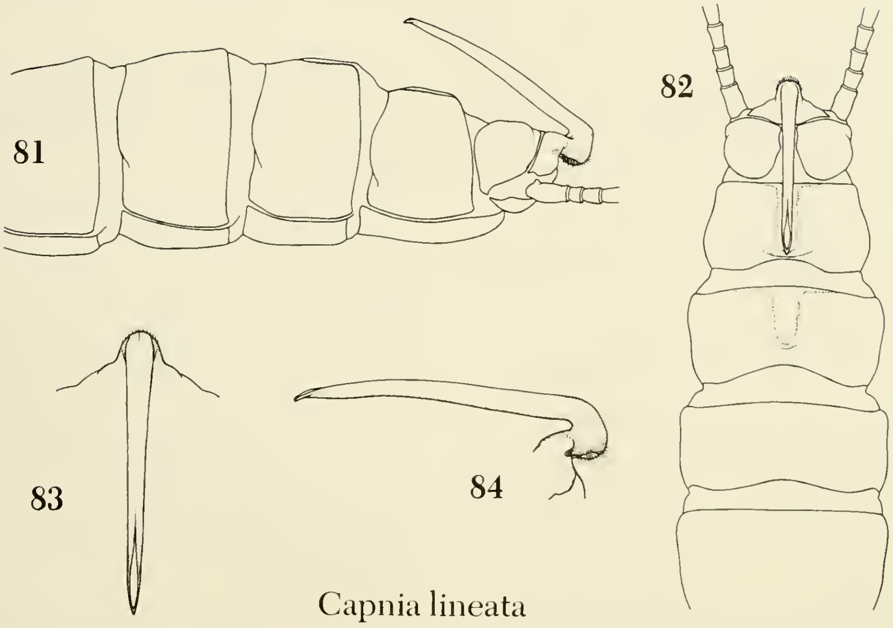
DISTRIBUTION.—COLORADO: Larimer Co., type locality and Young Gulch, above Ansel Watrous Campground, 1,768 m (5,800 feet); (2). 22 March–3 April.

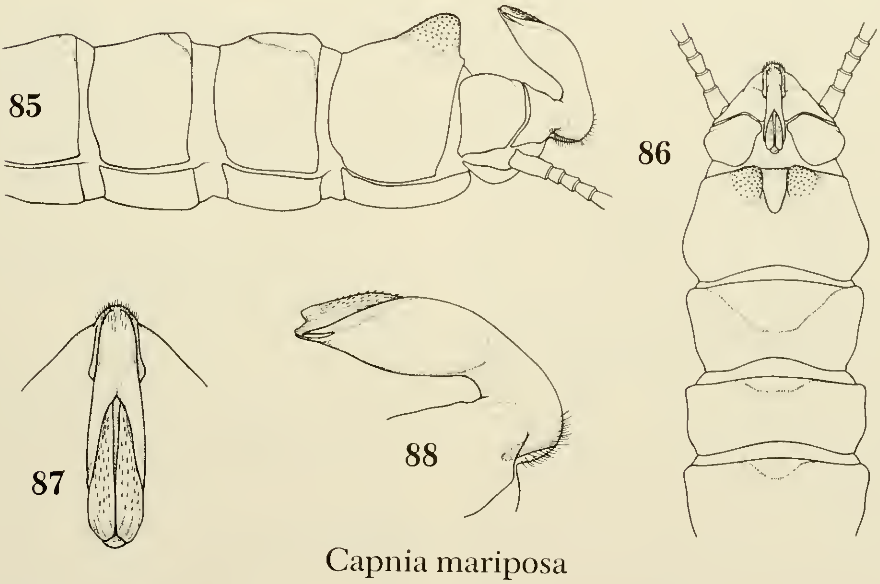
Capnia coyote Nelson & Baumann

Figs. 29–32, 217, map Fig. 267

Capnia coyote Nelson & Baumann 1987c: 487.

HOLOTYPE.—Male, California, Los Angeles Co., Little Rock Creek, Cooper Canyon Campground, San Gabriel Mountains, 31 March 1981, R. W. Baumann and J. A. Stanger; (USNM).





Figs. 81–84. *Capnia lineata* Hanson: 81, male terminalia, lateral; 82, male terminalia, dorsal; 83, male epiproct, dorsal; 84, male epiproct, lateral. Idaho, Latah Co., Little Boulder Creek, Little Boulder Creek Campground, 26 April 1985, R. W. Baumann and C. R. Nelson.

Figs. 85–88. *Capnia mariposa* Nelson & Baumann: 85, male terminalia, lateral; 86, male terminalia, dorsal; 87, male epiproct, dorsal; 88, male epiproct, lateral. California, Mariposa Co., Tuolumne River, Hwy 120, Tuolumne Meadows Campground, 27 June 1988, R. W. Baumann and J. A. Stanger.

DIAGNOSIS.—*Capnia coyote* is the sister species of *C. decepta*. The two are distinguished by the flatter upper surface of the epiproct and the longer gibbosity of the epiproct (as measured by the ratio of gibbosity length to greatest epiproct depth viewed from lateral aspect) in *C. coyote* compared to *C. decepta*. The females of *C. coyote* and *C. decepta* are indistinguishable.

DISTRIBUTION.—CALIFORNIA: Los Angeles Co.; San Bernardino Co.; (16). 27 December–17 March.

Capnia decepta (Banks)

Figs. 33–36, 209–210, 218, map Fig. 267

Arsapnia decepta Banks 1897: 22, 1907a: 15, 1907b: 329. Dodds and Hisaw 1925: 382.

Capnia decepta Needham and Claassen 1925: 264. Claassen 1940: 93. Hanson 1946: 239. Illies 1966: 135. Nebeker and Gaufin 1967b: 418, 1968: 2. Stark et al. 1973: 272, 1986: 385. Baumann et al. 1977: 70.

Capnia barbata Frison 1944: 153. Hanson 1946: 238. Gaufin 1964b: 309. Illies 1966: 132. Jewett 1966: 101. Nebeker and Gaufin 1967a: 246, 1967b: 418, 1968: 2. Stark et al. 1973: 272, 1986: 385. Zwick 1973: 371. Stewart et al. 1974: 514. Baumann et al. 1977: 64. Jacobi and Baumann 1983: 585. *New synonymy.*

HOLOTYPE.—Colorado, Larimer Co., Fort Collins, no date given, C. P. Gillette; (MCZ).

DIAGNOSIS.—This species is distinguished from other members of the group by having the bulb tapered uniformly and gradually to meet the tip when it is viewed from above. The base of the tip of *C. decepta* is wider relative to the width of the anterior declivity of the bulb than that of *C. tumida* and *C. pileata*. *Capnia decepta* is distinguished from *C. coyote* by having an epiproctal ratio of less than 2.0.

DISTRIBUTION.—ARIZONA: Apache Co.; Cochise Co.; Coconino Co.; Gila Co.; Graham Co.; Mohave Co.; Pima Co.; Santa Cruz Co.; Yavapai Co. BAJA CALIFORNIA: Sierra San Pedro Martir,CHIHUAHUA: Sierra Madre Occidental. COLORADO: Arapahoe Co.; Boulder Co.; Larimer Co. NEVADA: Clark Co. NEW MEXICO: Catron Co.; Grant Co.; Lincoln Co.; Rio Arriba Co.; San Miguel Co.; Santa Fe Co.; Sierra Co.; Socorro Co.; Taos Co.; Torrance Co.; (650). 27 December–24 April.

NOTE.—An Alberta record (Banks 1907b) of this species is far from any other known records. This specimen was not examined during this study but probably represents a female of *C. coloradensis*.

Capnia pileata Jewett

Figs. 125–128, 239, map Fig. 268

Capnia pileata Jewett 1966: 104. Zwick 1973: 77. Ricker and Scudder 1975: 339. Stark et al. 1986: 385.

Capnia tumida Frison 1942: 65. Ricker 1943: 98. Jewett 1959: 48.

HOLOTYPE.—Male (and female allotype), Portland, Oregon, Johnson Creek at 82nd Street, S. G. Jewett, Jr., 3 February 1939; (INHS).

DIAGNOSIS.—The male is distinguished from other species in the group by the concave anterior declivity of the epiproct, the presence of bristles forming a transverse row on a carina along the upper edge of the anterior declivity, and the concentration of the swelling of the bulb near that same region as opposed to the swollen area located nearer the neck region as in *C. tumida*.

The female differs from others in the group in the fusion of the anterior margin of the subgenital plate with the posterior margin of sternum 7.

DISTRIBUTION.—BRITISH COLUMBIA: Vancouver Island: Nanaimo, creeks and Millstone River. CALIFORNIA: Shasta Co.; Siskiyou Co. OREGON: Benton Co.; Clackamas Co.; Columbia Co.; Josephine Co.; Multnomah Co.; Yamhill Co.; (100). 15 January–10 April.

Capnia sequoia Nelson & Baumann

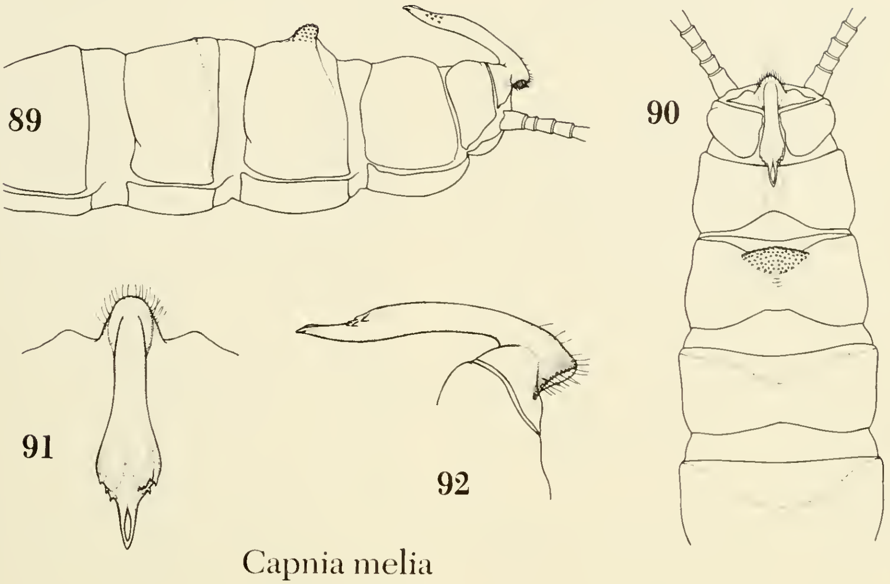
Figs. 149–152, 245, map Fig. 268

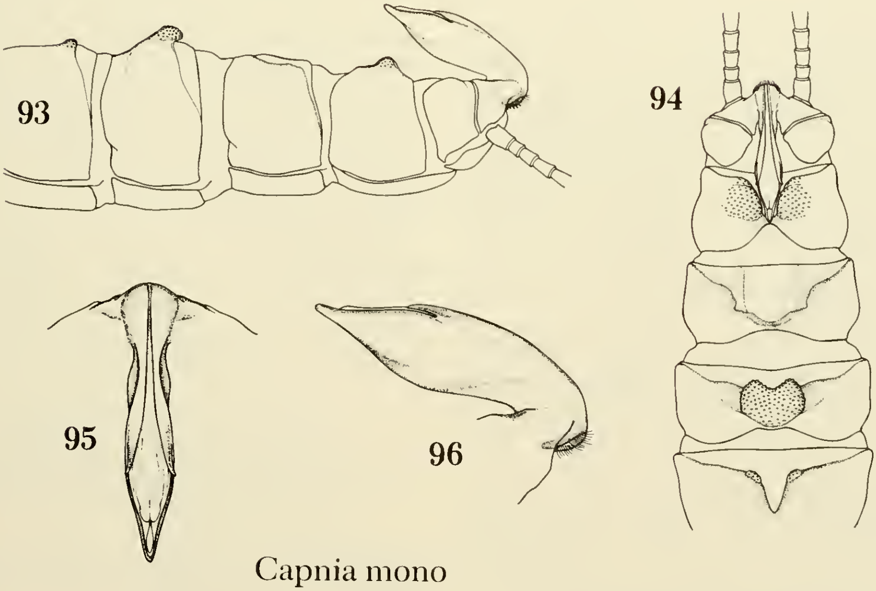
Capnia sequoia Nelson & Baumann 1987c: 489. Nelson & Baumann 1987d: 224.

HOLOTYPE.—Male (and female allotype), California, Tuolumne Co., Ackerson Creek, Evergreen Lodge Road, 18 March 1985, R. W. Baumann and C. R. Nelson; (USNM).

DIAGNOSIS.—This species is most closely related to *C. tumida*, from which males differ in the following characters: the anterior declivity of *C. sequoia* never has spines while that of *C. tumida* is variable in having few to many spines, from the lateral aspect this species (Fig. 152) is flatter and lacks a distinct carinate ridge at the junction of the tip and the bulb on the anterior declivity. The females of the two species are indistinguishable.

DISTRIBUTION.—CALIFORNIA: Fresno Co.; Mariposa Co.; Tulare Co.; Tuolumne Co.; (62). 16 December–22 June.





Figs. 89–92. *Capnia melia* Frison: 89, male terminalia, lateral; 90, male terminalia, dorsal; 91, male epiproct, dorsal; 92, male epiproct, lateral. Oregon, Clackamas Co., Wildcat Creek, Hwy 36, 1 mile east of Alder Creek, 2 March 1984, R. W. Baumann, C. R. Nelson, and G. R. Fiala.

Figs. 93–96. *Capnia mono* Nelson & Baumann: 93, male terminalia, lateral; 94, male terminalia, dorsal; 95, male epiproct, dorsal; 96, male epiproct, lateral. California, Mono Co., Slinkard Creek, 2 miles north of Topaz, 5 November 1983, W. D. Shepard, reared from nymph in laboratory.

Capnia teresa Claassen

Figs. 165–168, 249, map Fig. 267

Capnia teresa Claassen 1924: 54, 1940: 95. Needham and Claassen 1925: 262. Hanson 1946: 239. Jewett 1956: 170, 1960: 146. Illies 1966: 147. Stark et al. 1986: 385.

HOLOTYPE.—Male, California, Los Angeles Co., Evey Canyon, Claremont, 15 October 1922; (CU, vial located, specimen lost).

DIAGNOSIS.—The male of this species is distinguishable from other members of the group by the nearly spherical bulb of the epiproct and the presence of bristles on the sides of the bulb near the posterior declivity. The tip of the epiproct is very thin, nearly bristlelike in this species. Other species in the group lack these characters. The female is readily separated from others in the group by the notched subgenital plate.

FEMALE DESCRIPTION.—Wings macropterous, length of forewing 6.9 mm; length of body 6.8 mm. General appearance similar to male. Dorsal membranous stripe from abdominal tergum 1 to 8. Abdominal tergum 8 with small, triangular sclerite located centrally on midline of tergum. Subgenital plate consisting of a recessed, bilobed, sclerotized flap, divided by a medial indentation, one-third to one-half the length of the sclerotized portion of the plate. Darkest portion of subgenital plate forming a medial triangle with the apex directed posteriorly. Subgenital plate separated from sternum 7 by unsclerotized intersegmental membrane. Pleural membrane of abdominal segment 7 bearing a small sclerite.

MATERIAL.—Female, California, Riverside Co., San Jacinto Mountains, Herkey Creek, Herkey Creek Campground, 19 January 1985, R. W. Baumann and C. R. Nelson; (BYU).

DISTRIBUTION.—CALIFORNIA: Riverside Co.; San Bernardino Co.; (300). 24 December–20 March.

Capnia tumida Claassen

Figs. 169–172, 250, map Fig. 268

Capnia tumida Claassen 1924: 56, 1940: 95. Needham and Claassen 1925: 261. Frison 1942: 65 (see Jewett 1966). Ricker 1943: 98 (see *C. pileata*). Hanson 1946: 239. Jewett 1956: 170, 1959: 48, 1960: 146, 1966: 106. Ricker 1965: 68. Illies 1966: 148. Zwick 1973: 379. Stark et al. 1986: 385.

HOLOTYPE.—Male, California, Plumas Co., Sunnyside Mine near Seneca, 25–26 December 1922, H.S. Barber; (USNM). Female allotype, California, El Dorado Co., creek about 5 miles west of Pyramid Campground, Highway 50, 22 May 1964, S. G. Jewett, Jr.; (CAS).

DIAGNOSIS.—The male of *C. tumida* is distinguished from other members of the group by the shape of the epiproct bulb and its anterior declivity. The bulb ends distally with the demarcation of the bulb from the base of the tip being abrupt, the width of the base of the tip being much narrower than the distal face of the bulb (from dorsal aspect, Fig. 171). These characters distinguish *C. tumida* from *C. decepta* and *C. coyote*. It is separated from the related *C. pileata* by the following characters: the anterior declivity is convex or flat, never concave as in *C. pileata*, the bristles of the anterior declivity are not situated on a well-defined carina, and the swollen portion of the bulb is located near the center of its length, not concentrated near the anterior declivity as in *C. pileata*. It differs from *C. sequoia* in having spines on the anterior declivity and having a more angular anterior declivity.

The female is distinguished from related species by its subgenital plate, which is square or nearly square and not fused to sternum 7 along its anterior margin. The subgenital plate is longer than wide in *C. decepta*, notched in *C. teresa*, and fused to sternum 7 in *C. pileata*. The females of *C. tumida* and *C. sequoia* are indistinguishable.

DISTRIBUTION.—CALIFORNIA: Alpine Co.; El Dorado Co.; Placer Co.; Plumas Co.; Sacramento Co.; Shasta Co.; Sierra Co.; Siskiyou Co.; Tehama Co. NEVADA: Washoe Co.; (200). 9 December–22 May.

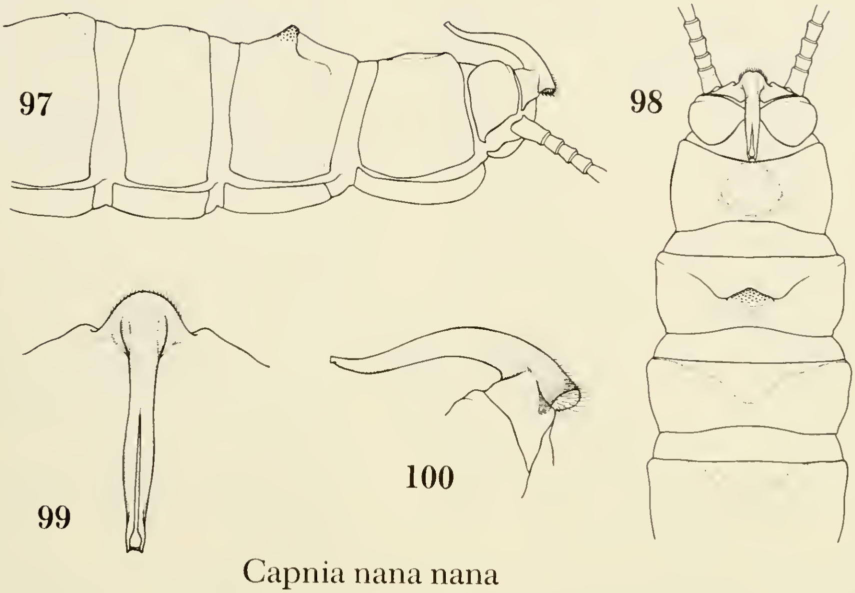
Capnia utahensis Gaufin & Jewett

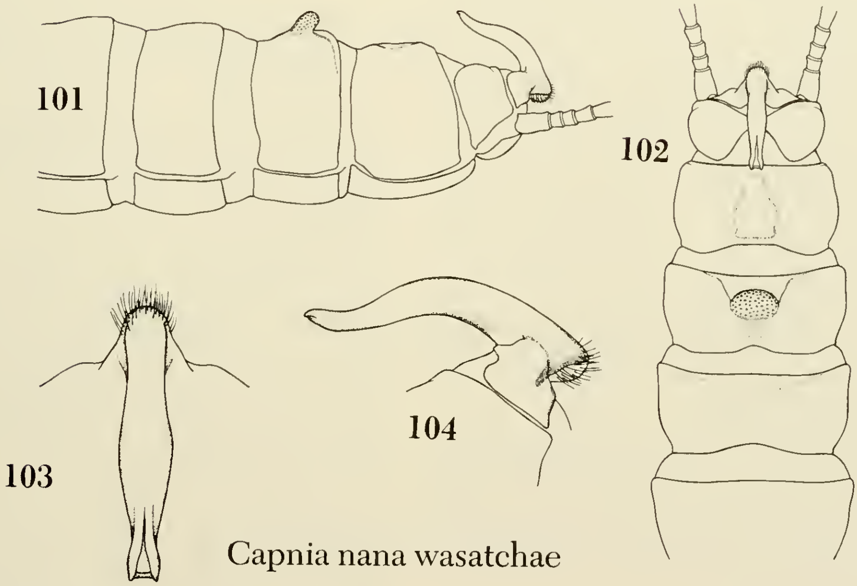
Figs. 181–184, 253, map Fig. 268

Capnia utahensis Gaufin and Jewett 1962: 69. Gaufin 1964a: 223, 1966: 49. Illies 1966: 148. Nebeker and Gaufin 1967a: 418, 1968: 3. Baumann et al. 1977: 74. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), Utah, Beaver Co., Beaver Creek, 21 March 1959, A. R. Gaufin; (CAS).

DIAGNOSIS.—This species is most closely allied to *C. sequoia*, from which it differs in having the tergal knob on segment 7 much reduced or virtually absent and the epiproct much flatter and narrower. The females are not easily separated, but the subgenital plate of this species is slightly narrower. Current data indicate that the distributions of the two


97
98
99
100
Capnia nana nana


101
102
103
104
Capnia nana wasatchae

Figs. 97–100. *Capnia nana nana* Claassen: 97, male terminalia, lateral; 98, male terminalia, dorsal; 99, male epiproct, dorsal; 100, male epiproct, lateral. British Columbia, Terrace, 1936, M. E. Hippisley.

Figs. 101–104. *Capnia nana wasatchae* Nebeker & Gaufin: 101, male terminalia, lateral; 102, male terminalia, dorsal; 103, male epiproct, dorsal; 104, male epiproct, lateral. Utah, Cache Co., Logan Canyon, Springhollow, tributary of Logan River, 4 January 1984, C. R. Nelson and S. A. Wells.

species do not overlap. However, more collecting needs to be done on the west slope of the southern Sierra Nevada before the distributional limits of these two species are definitive in that area.

DISTRIBUTION.—CALIFORNIA: Inyo Co.; Kern Co., Cedar Creek, Highway 155, Cedar Creek Campground, 2 May 1981, Baumann and Stanger; same locality, 15 March 1985, Baumann and Nelson; Kern Co., Slick Rock Creek, Highway 155, west of Greenhorn Summit, 15 March 1985, Baumann and Nelson; Mono Co.; Tulare Co., Soda Creek, Highway 190, west of Pierpoint Springs, 16 March 1985, Baumann and Nelson. NEVADA: Esmeralda Co.; Lander Co.; Nye Co.; White Pine Co. UTAH: Beaver Co.; Iron Co.; Juab Co.; Millard Co.; Piute Co.; Sevier Co.; Utah Co.; Washington Co.; (865). 28 December–14 May.

Excavata Group

This group includes three species, *C. cheama* Ricker, *C. excavata* Claassen, and *C. uintahi* Gaufin. The group is unique among *Capnia* in having the epiproct produced as a broad, flat, lateral flange at about midlength of the shaft. This group is most closely allied to the *nana* group, based on the presence of a well-developed tergal knob on segment 8. The tergal knob of this group is more highly modified than that of the *nana* group, and in unrelaxed specimens it is common for the knob to obscure the tip of the epiproct up to the point of the lateral flange. For proper species identification the specimens should be relaxed so that details of the tip of the epiproct are visible.

DISTRIBUTION.—The distributional area covered by the group is large, ranging from Alaska and Alberta on the north to central California and Colorado on the south. The three species in the group are allopatric and widely separated.

Key to the Males of the Excavata Group

1. Knob on tergum 8 divided into two distinct, tuberculate knobs in lateral view; epiproct with tip short and pointed (Figs. 41, 44); in Pacific coast states and western British Columbia .... *excavata* Claassen

— Knob on tergum 8 not divided, a single knob in lateral view; epiproct with tip longer and blunt; ranging farther inland 2

2(1). Lateral flange of epiproct very broad and flattened (Fig. 175); tip of epiproct simple, not bearing a projection on upper margin (Fig. 176); inhabiting small creeks in some parts of the central Rocky Mountains and adjacent areas .... *uintahi* Gaufin

— Lateral flange of epiproct not so broad and flat (Fig. 19); tip of epiproct bearing a small projection when viewed laterally (Fig. 20); in large rivers near the border of Montana and British Columbia .... *cheama* Ricker

Key to the Females of the Excavata Group

1. Subgenital plate with posterior margin divided medially (Fig. 214) .... *cheama*

— Subgenital plate not divided medially 2

2(1). Subgenital plate darkly sclerotized throughout, posterior margin not recessed but produced to a point medially, anterior margin of plate entire (Fig. 220) .... *excavata*

— Subgenital plate not darkly sclerotized, posterior margin recessed and not produced medially, anterior margin of plate with a medial notch (Fig. 251) .... *uintahi*

Capnia cheama Ricker

Figs. 17–20, 214, map Fig. 266

Capnia cheama Ricker 1965: 484. Nebeker and Gaufin 1967a: 418, 1968: 2. Zwick 1973: 372. Ricker and Scudder 1975: 338. Baumann et al. 1977: 66. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), British Columbia, Fraser River Bridge near Agassiz, 14 March 1958, W. E. Ricker; (CNC).

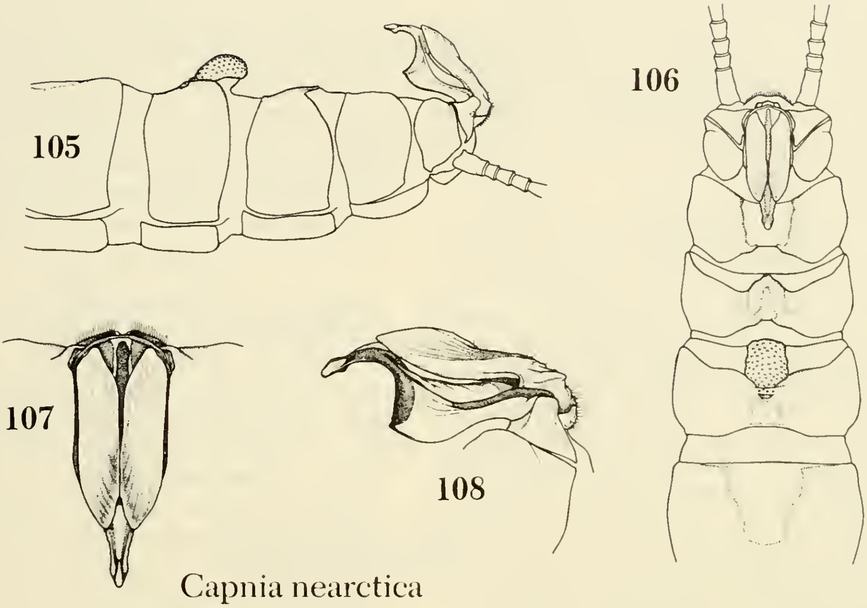
DIAGNOSIS.—The male of this species is separated from that of *C. uintahi* by the narrower lateral flange of the epiproct and from that of *C. excavata* by the undivided tergal knob on segment 8. The female of *C. cheama* has a medial notch in the posterior margin of the subgenital plate, a character shared only with the female of *C. teresa*, the range of which is farther south.

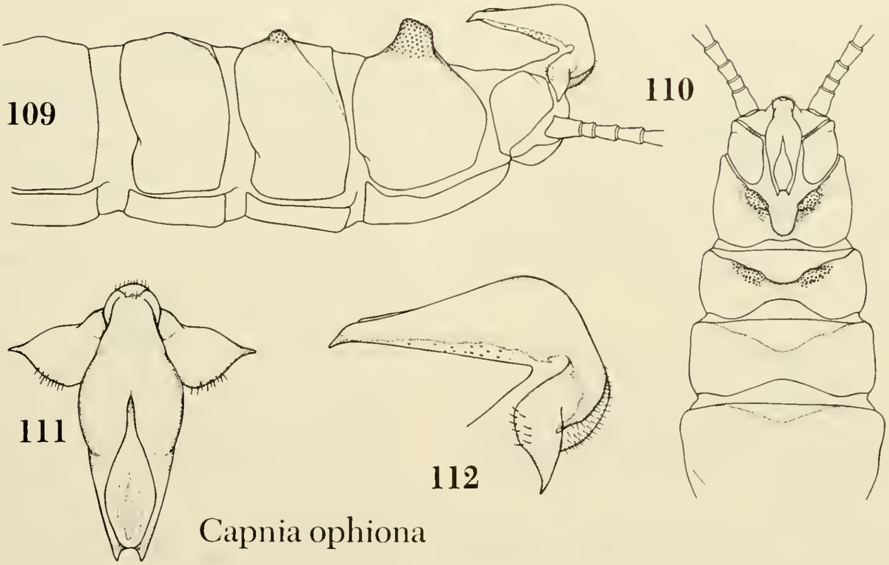
DISTRIBUTION.—ALBERTA: Athabasca River, Jasper National Park. BRITISH COLUMBIA: Fraser River, Elk River. MONTANA: Lincoln Co., Kootenai River, near Libby; (100). 14 March–1 May.

Capnia excavata Claassen

Figs. 41–44, 220, map Fig. 266

Capnia excavata Claassen 1924: 47, 1940: 93. Needham and Claassen 1925: 260. Frison 1937: 87. Ricker 1939: 21, 1943: 98, 1964: 68. Hanson 1946: 239. Jewett 1956: 170, 1959: 45, 1960: 145. Illies 1966: 137. Ricker and Scudder 1975: 339. Stark et al. 1986: 385.


105
106
107
108
Capnia nearctica


109
110
111
112
Capnia ophiona

Figs. 105–108. *Capnia nearctica* Banks: 105, male terminalia, lateral; 106, male terminalia, dorsal; 107, male epiproct, dorsal; 108, male epiproct, lateral. Northwest Territories, Keewatin District, Baffin Island, Nettilling Lake, 6 July 1956.

Figs. 109–112. *Capnia ophiona* Nelson & Baumann: 109, male terminalia, lateral; 110, male terminalia, dorsal; 111, male epiproct, dorsal; 112, male epiproct, lateral. California, Butte Co., Butte Creek, Butte Meadows Campground, 15 February 1985, R. W. Baumann and C. R. Nelson.

HOLOTYPE.—Male, California, Plumas Co., Feather River Canyon near Caribou, 24 January 1923, H. S. Barber; (USNM).

DIAGNOSIS.—This species is distinguished from others in the group by the presence of a divided tergal knob (Fig. 41) on segment 8 of the male and the darkened subgenital plate of the female, which is produced posteromedially.

DISTRIBUTION.—ALASKA: Anan Creek, southeast Wrangell, Bradfield Canal; Kowee Creek, northwest Juneau, Berners Bay; Muir Inlet. BRITISH COLUMBIA: Cameron Creek; Fraser River, Agassiz; Garibaldi Provincial Park; Harrison River at Cheheilus Indian Reserve; Nicolum River Provincial Park; Queen Charlotte Islands, Moresby Island, Browns Cabin Creek; Queen Charlotte Islands, Graham Island, Massett Inlet, Mamin River; Silverhope Creek; Vancouver Island, Courtenay and Haslom creeks (near Nanaimo); Vedder Crossing. CALIFORNIA: Butte Co.; El Dorado Co.; Humboldt Co.; Marin Co.; Mendocino Co.; Nevada Co.; Placer Co.; Plumas Co.; Shasta Co.; Sierra Co.; Siskiyou Co.; Sonoma Co.; Tehama Co.; Tuolumne Co. OREGON: Benton Co.; Clackamas Co.; Clatsop Co.; Columbia Co.; Curry Co.; Douglas Co.; Hood River Co.; Josephine Co.; Lane Co.; Linn Co.; Marion Co.; Multnomah Co.; Polk Co.; Wasco Co., Washington Co.; Yamhill Co. WASHINGTON: Clark Co.; Cowlitz Co.; Grays Harbor Co.; Jefferson Co.; King Co.; Klickitat Co.; Lewis Co.; Pierce Co.; Skagit Co.; Skamania Co.; Wahkiakum Co.; (1645). 24 January–17 April.

Capnia uintahi Gaufin

Figs. 173–176, 251, map Fig. 266

Capnia uintahi Gaufin 1964a: 223, 1964b: 307. Gaufin et al. 1966: 49. Nebeker and Gaufin 1967a: 418, 1967b: 244, 1968: 3. Baumann and Gaufin 1971: 108. Baumann et al. 1977. Zwick 1973: 379. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), Utah, Wasatch Co.; Provo River, Stewarts Ranch, 2 March 1949; (USNM).

DIAGNOSIS.—The extremely broad and flattened lateral flange on the epiproct easily distinguishes this species from all other *Capnia*. This species is most closely allied to *C. cheama*, from which it may be separated by the absence of a projection on the upper margin of the tip of the epiproct that is present in *C. cheama*. The females may be recognized as having a pronounced notch on the anterior margin of the subgenital plate.

DISTRIBUTION.—COLORADO: Summit Co.; Cow Creek, Route 9, near mile marker 125, Green Mountain Reservoir, 9 March 1985. IDAHO: Bannock Co.; Bonneville Co.; Caribou Co.; Franklin Co.; Oneida Co. NEVADA: Elko Co.; Lander Co.; Nye Co.; White Pine Co. UTAH: Davis Co.; Salt Lake Co.; Summit Co.; Wasatch Co.; Weber Co. WYOMING: Lincoln Co.; (550). 16 February–23 August.

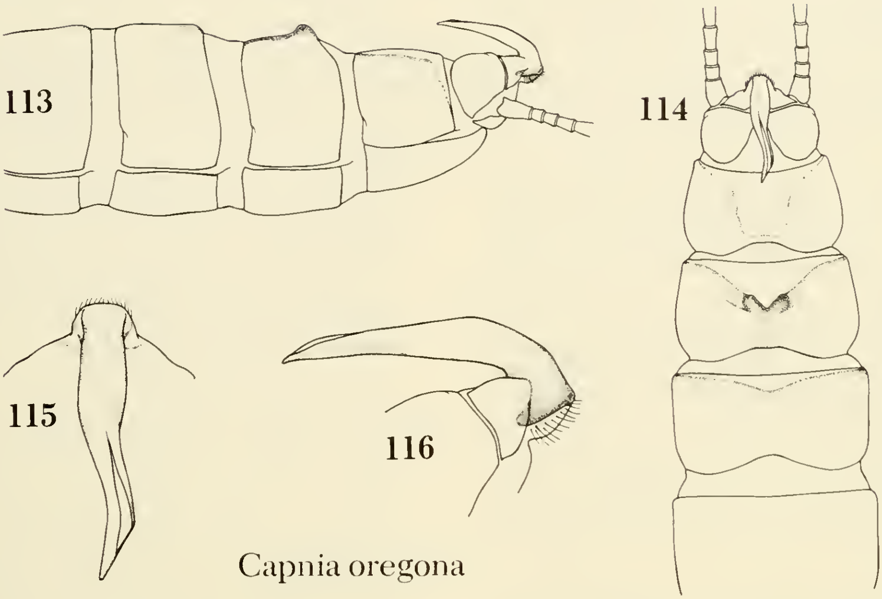
Gracilaria Group

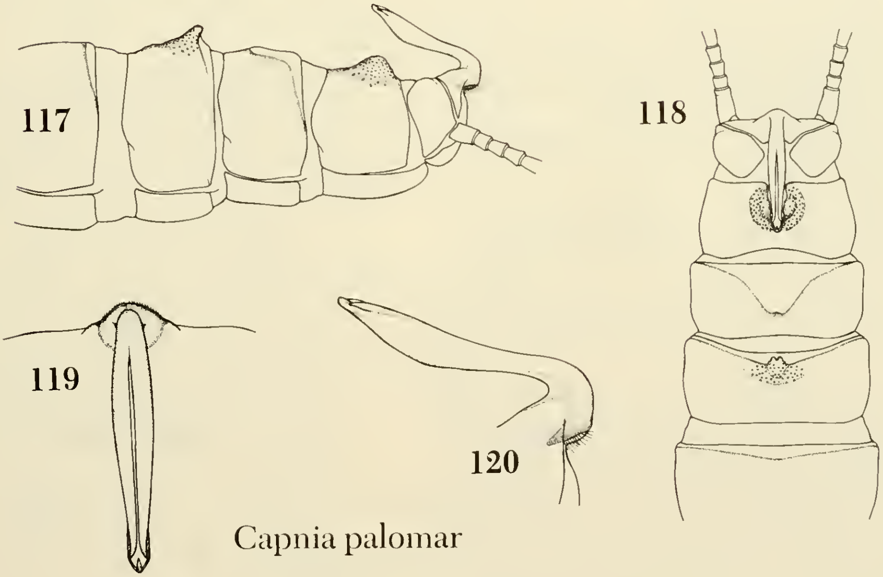
The *C. gracilaria* group consists of four species: *Capnia elongata*, *C. gracilaria*, *C. lacustra*, and *C. promota*. These four species are united as a group by the elongate, tubelike epiproct, the presence of a tergal knob, modified to varying degrees, on abdominal segment 7, and the compoundly curved epiproct (curving upward at base and then downward before returning upward). The combination of characters of the compoundly curved epiproct and a knob on tergum 7 (except in *C. lacustra*) will differentiate the members of this group from all other North American *Capnia*. The tergal knob of *C. gracilaria* and *C. promota* is small and not significantly modified. These two species, along with *C. lacustra*, have very long curving epiprocts that should not be confused with those of other species. The genus *Mesocapnia* has an elongate epiproct, but it curves upward or is straight along the length and, in *Mesocapnia*, there are no tergal knobs. Females have a simple subgenital plate, the posterior margin of which is darkened and often tridentate.

DISTRIBUTION.—This group is very widely distributed in the western United States, particularly *C. gracilaria*. Members have been collected from Baja California to Alaska and eastward to the limits of the mountains. Inland the species in this group have been collected from Alberta to New Mexico. No representatives of the group are found in the Sierra Nevada south of the Lake Tahoe region. *Capnia elongata*, *C. lacustra*, and *C. promota* are limited in distribution to the northern Sierra Nevada and the Cascades. The members of this group are often the "dominant" capniid in the streams in their range.

Key to the Males of the Gracilaria Group

1. Abdominal terga lacking knobs, epiproct with angulate bend near base in lateral view (Figs.


113
114
115
116
Capnia oregona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119
120
Capnia palomar

Figs. 113–116. *Capnia oregona* Frison: 113, male terminalia, lateral; 114, male terminalia, dorsal; 115, male epiproct, dorsal; 116, male epiproct, lateral. Oregon, Linn Co., Gordon Meadows, 4,000 feet, 18 July 1959, H. Hacker.

Figs. 117–120. *Capnia palomar* Nelson & Baumann: 117, male terminalia, lateral; 118, male terminalia, dorsal; 119, male epiproct, dorsal; 120, male epiproct, lateral. California, San Diego Co., Palomar Mountain, Fry Creek, Road S–6, Fry Creek Campground, 18 January 1985, R. W. Baumann and C. R. Nelson.

73, 76); inhabiting depths of Lake Tahoe .... *lacustra* Jewett

— Abdominal tergum 7 with modified knob; base of epiproct evenly curved, not angulate; widespread 2

2(1). Tube of epiproct of uniform height throughout length or with greatest height on distal third (lateral view, Figs. 56, 132); terga 7 and 8 both bearing small tuberculate knobs (Figs. 53, 129) 3

— Tube of epiproct with an expanded region at half its length which then tapers to a narrow tip (Fig. 40); tergum 7 bearing a large, prominent, tuberculate knob, knob not present on tergum 8 (Fig. 37) .... *elongata* Claassen

3(2). Epiproct of uniform width throughout its length (Figs. 54, 55); tip of epiproct usually not bent distinctly upward at tip (Fig. 56); ranging inland from Cascade Mountains south of British Columbia to New Mexico ...... *gracilaria* Claassen

— Epiproct with distal one-half expanded laterally to double width of epiproct (Fig. 131); epiproct with tip always bent upward (Fig. 132); ranging more coastal, in the Cascades and Sierra Nevada .... *promota* Frison

Key to the Females of the Gracilaria Group

1. Subgenital plate darkened throughout length, joined to sternum 7 by a sclerotized bridge that is also darkened (Fig. 219) .... *elongata*

— Subgenital plate with dark area limited to posterior margin; sterna 7 and 8 separated by intersegmental membrane, not joined by a sclerotized bridge 2

2(1). Inhabiting depths of Lake Tahoe on border of California and Nevada (Fig. 227) .... *lacustra*

— Widespread 3

3(2). Distribution east of the Cascade Mountains in the Rocky Mountains and Great Basin (Fig. 222) .... *gracilaria*

— Distribution limited to streams draining the northern Cascade and Coast Ranges (Fig. 240) .... *promota*

NOTES.—The females of *C. gracilaria* and *C. promota* are morphologically indistinguishable, and both species have been collected in the same stream on the same day in south central Washington. The configuration of the subgenital plate of females of *C. lacustra* (Fig. 227) is within the variation seen in *C. gracilaria* and *C. promota* (Figs. 222, 240).

Capnia elongata Claassen

Figs. 37–40, 219, map Fig. 270

Capnia elongata Claassen 1924: 56, 1940: 93. Needham and Claassen 1925: 260. Ricker 1943: 99. Hanson 1946: 239. Jewett 1956: 170, 1959: 45, 1960: 145. Illies 1966: 136. Nebeker and Gaufin 1967b: 419, 1968: 3. Zwick 1973: 373. Ricker and Scudder 1975: 338. Stark et al. 1986: 385.

HOLOTYPE.—Male, California, Plumas Co., near Caribou, 24 January 1922, H. S. Barber; (USNM).

DIAGNOSIS.—The male of this species is distinguished from others in the group by the large, modified tergal knob on segment 7, the absence of a knob on tergum 8, and the tubelike epiproct, which is thick basally and tapers toward the tip. The female may be separated from others in the group by sterna 7 and 8 being joined by a broad bridge. This female may be confused with some of the females in the Barberi group in this respect but may be separated from them by its subgenital plate, which is much lighter in color.

DISTRIBUTION.—BRITISH COLUMBIA: Fraser River, Agassiz; Mamquam River, tributary Squamish River; Vedder Crossing; Wahleach Creek, tributary Fraser River. CALIFORNIA: Alpine Co.; El Dorado Co.; Mariposa Co.; Nevada Co.; Placer Co.; Plumas Co.; Sierra Co.; Siskiyou Co.; Tehama Co.; Trinity Co.; Tuolumne Co. OREGON: Clackamas Co.; Jackson Co.; Linn Co.; Marion Co.; Multnomah Co. WASHINGTON: Cowlitz Co.; Lewis Co.; Pierce Co.; Skagit Co.; (1380). 18 January–14 June.

NOTES.—Hoppe (1938) described and produced a figure of a female that could fit either the female of *C. gracilaria* or *C. promota;* in any case the female described and figured by Ricker (1943) is indeed that of *C. elongata*.

Capnia gracilaria Claassen

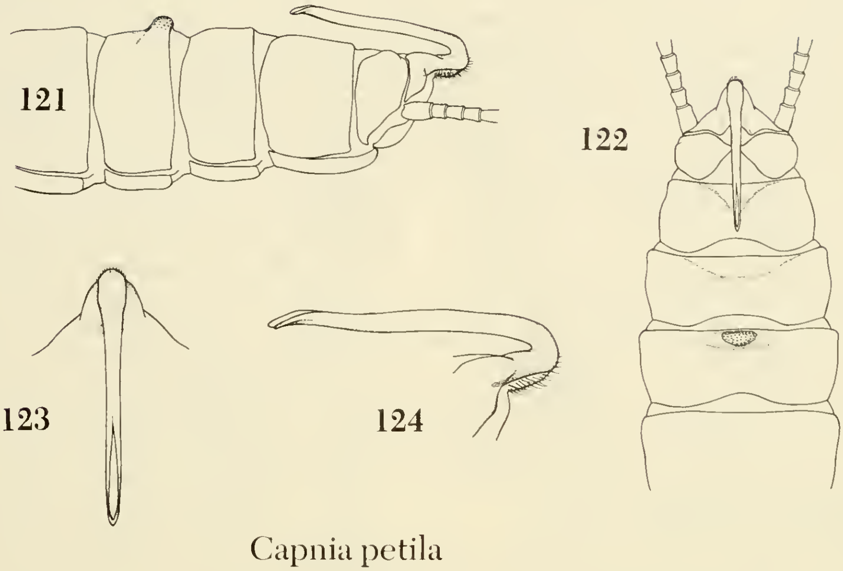
Figs. 53–56, 222, map Fig. 269

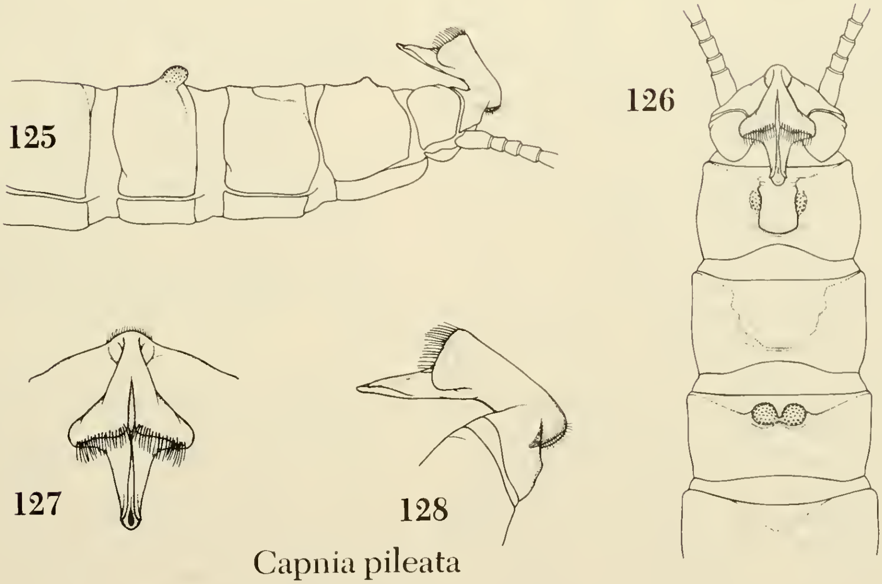
Capnia gracilaria Claassen 1924: 57, 1940: 93. Needham and Claassen 1925: 258. Ricker 1939: 21, 1943: 99. Hanson 1946: 239. Gaufin 1955: 118. Jewett 1959: 45, 1960: 145. Illies 1966: 138. Knight and Gaufin 1966: 669, 1967: 348. Nebeker and Gaufin 1966: 42, 1967b: 419, 1968: 3. Hitchcock 1969: 314. Newell 1970: 50. Nebeker 1971: 27. Zwick 1973: 373. Baumann et al. 1977: 70. Stark et al. 1986: 385.

Capnia elongata Knowlton and Harmston 1938: 284. Castle 1939: 211. Ricker 1939: 21. Gaufin 1955: 118. Gaufin et al. 1966: 46. Newell 1970: 50.

HOLOTYPE.—Male, Aweme, Manitoba, 28 April 1907, N. Criddle; (CU).

DIAGNOSIS.—The males of this widespread and common species may be confused with those of other members of the group. This species has a tubelike epiproct that is uniformly round in cross section from base to tip. The epiproct of *C. promota* is expanded laterally on the distal third so that a cross section


121
122
123
124
Capnia petila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128
Capnia pileata

Figs. 121–124. *Capnia petila* Jewett: 121, male terminalia, lateral; 122, male terminalia, dorsal; 123, male epiproct, dorsal; 124, male epiproct, lateral. Utah, Box Elder Co., Raft River Mountains, Fisher Creek, 29 March 1979, R. W. Baumann and G. M. Webb.

Figs. 125–128. *Capnia pileata* Jewett: 125, male terminalia, lateral; 126, male terminalia, dorsal; 127, male epiproct, dorsal; 128, male epiproct, lateral. Oregon, Clackamas Co., 0.6 miles north of Marquam, 15 January 1967, S. G. Jewett, Jr.

through the epiproct would produce an oval with the long axis horizontal. The epiproct of *C. elongata* is expanded in a vertical plane on its basal half; a cross section in this area would produce an oval with the long axis arranged vertically. The females have a relatively simple subgenital plate that is roughly square and darkened only along the posterior margin. The posterior margin has a short medial extension of varying length and often a pair of shorter extensions on either side of this medial tooth; these extensions are missing on some specimens, giving the impression of a smoothly rounded plate apically. The female of *C. elongata* is separated from those of this species by the fused sterna 7 and 8. The females of *C. gracilaria*, *C. lacustra*, and *C. promota* are structurally indistinguishable, except that *C. lacustra* is totally wingless. Thus, any identification of these species must be based on the male characteristics.

DISTRIBUTION.—ALASKA: Eklutna; Girdwood (near Anchorage). ALBERTA: Jasper National Park; Banff National Park. BAJA CALIFORNIA: Sierra San Pedro Martir. BRITISH COLUMBIA: Cultus Lake, Moyie River; Garibaldi Lake; Keremeos Creek; Manning Provincial Park; Penticton, Ellis Creek; Shatford Creek; Shingle Creek. CALIFORNIA: Los Angeles Co.; Modoc Co.; San Mateo Co.; Santa Clara Co.; Siskiyou Co.; Trinity Co.; Ventura Co. COLORADO: Archuleta Co.; Clear Creek Co.; Gilpin Co.; Gunnison Co.; Hinsdale Co.; Lake Co.; La Plata Co.; Larimer Co.; Las Animas Co.; Montrose Co.; Ouray Co.; Routt Co.; Summit Co. IDAHO: Ada Co.; Adams Co.; Bannock Co.; Bear Lake Co.; Blaine Co.; Boise Co.; Bonner Co.; Bonneville Co.; Boundary Co.; Caribou Co.; Cassia Co.; Clearwater Co.; Custer Co.; Franklin Co.; Fremont Co.; Idaho Co.; Jefferson Co.; Latah Co.; Lemhi Co.; Lewis Co.; Nez Pierce Co.; Shoshone Co.; Teton Co.; Twin Falls Co.; Valley Co.; Washington Co. MONTANA: Broadwater Co.; Flathead Co.; Gallatin Co.; Glacier Co.; Granite Co.; Lake Co.; Lewis and Clark Co.; Lincoln Co.; Meagher Co.; Missoula Co.; Park Co.; Ravalli Co.; Sanders Co. NEVADA: Elko Co.; Humboldt Co.; White Pine Co. NEW MEXICO: Colfax Co.; Grant Co.; Lincoln Co.; Sandoval Co.; San Miguel Co.; Santa Fe Co.; Taos Co. OREGON: Baker Co.; Deschutes Co.; Hood River Co.; Josephine Co.; Klamath Co.; Umatilla Co.; Union Co.; Wallowa Co.; Wasco Co. SOUTH DAKOTA: Lawrence Co. UTAH: Beaver Co.; Box Elder Co.; Cache Co.; Carbon Co.; Daggett Co.; Davis Co.; Duchesne Co.; Emery Co.; Garfield Co.; Grand Co.; Iron Co.; Juab Co.; Kane Co.; Millard Co.; Morgan Co.; Piute Co.; Rich Co.; Salt Lake Co.; San Juan Co.; Sanpete Co.; Sevier Co.; Summit Co.; Tooele Co.; Uintah Co.; Utah Co.; Wasatch Co.; Washington Co.; Wayne Co.; Weber Co. WASHINGTON: Asotin Co.; Garfield Co.; King Co.; Kittitas Co.; Klickitat Co.; Skamania Co.; Whitman Co.; Yakima Co. WYOMING: Albany Co.; Lincoln Co.; Park Co.; Platte Co.; Sublette Co.; Teton Co. YUKON TERRITORY: Christmas and Boutellier creeks, near Kluane; Klondike Highway, Moose Creek Campground; North Klondike River, Tombstone Camp; Whitehorse, Wolf Creek Campground; (3512). 26 December–14 July.

NOTE.—This species is comparatively homogeneous throughout its range, but several populations vary in structural details of the epiproct. These include the populations in both northern and southern California. As noted earlier, *C. gracilaria* and *C. promota* occur sympatrically in some streams in central Washington.

Capnia lacustra Jewett

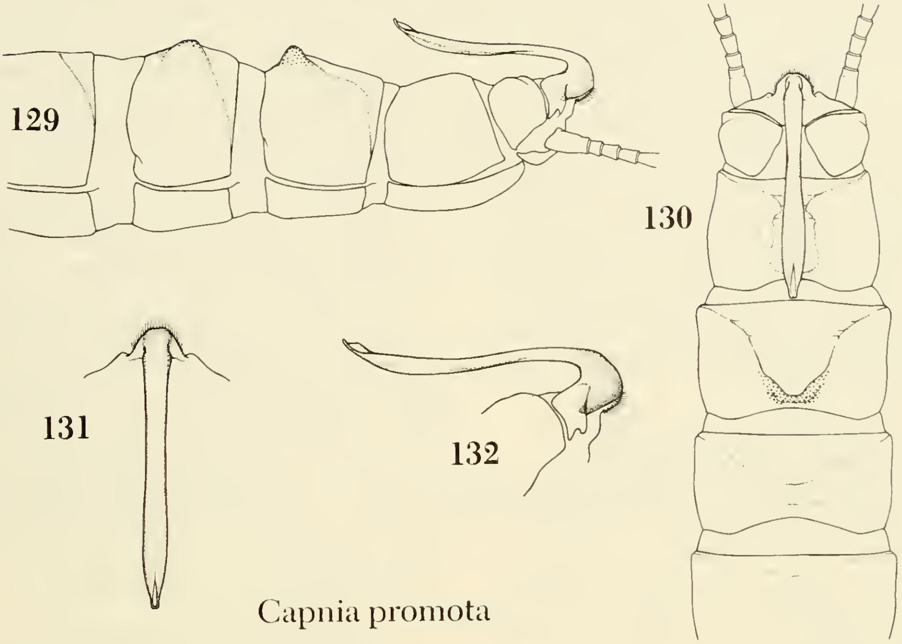
Figs. 73–76, 227, map Fig. 269

Capnia sp., Jewett 1963: 484.

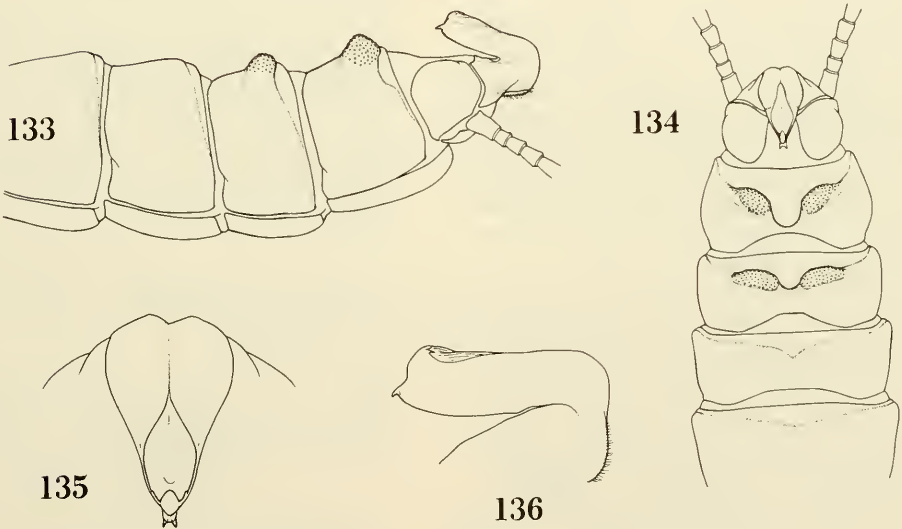
Capnia lacustra Jewett 1965: 5. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), Nevada, Douglas Co., bottom of Lake Tahoe at depth of 200–264 feet off Cave Rock, 22 and 28 May 1962, Cordone, Frantz, Weedlein; (CAS).

DIAGNOSIS.—This species is totally apterous. Another very apparent way of distinguishing this species from the others in the genus is that it is caught as the adult below the surface of Lake Tahoe. The epiproct of the male is unique in having an angular projection on the upper margin of the epiproct near the base (lateral view); all other similar species of the genus have the epiproct curving evenly forward in this area. This species appears to be an extremely derived member of the *gracilaria* group as based on the long, tubelike, compoundly curved epiproct. Males lack the modified tergal knob of the other members of the group. The female has the posterior margin of the subgenital plate resembling that of *C. gracilaria* and *C. promota*.



Capnia promota



Capnia quadrituberosa

Figs. 129–132. *Capnia promota* Frison: 129, male terminalia, lateral; 130, male terminalia, dorsal; 131, male epiproct, dorsal; 132, male epiproct, lateral. Oregon, Benton Co., Corvallis, Oak Creek, 1 January 1936.

Figs. 133–136. *Capnia quadrituberosa* Hitchcock: 133, male terminalia, lateral; 134 male terminalia, dorsal; 135, male epiproct, dorsal; 136, male epiproct, lateral. California, Butte Co., small stream north of Oroville near Garden Drive, 15 February 1985, R. W. Baumann and C. R. Nelson.

DISTRIBUTION.—This species has been collected at several locations in Lake Tahoe, both in California and Nevada at depths of 100–422 feet. The specimens were obtained by dredging beds of *Chara* sp.; (32). April–December.

NOTES.—This species is the only stonefly in the world known to be fully aquatic in the adult stage. This species has not been collected again despite our intense efforts using the facilities of the University of California, Davis Research Station on Lake Tahoe. An additional species of capniid, *Utacapnia tahoensis* (Nebeker & Gaufin), is also present in Lake Tahoe and can be readily collected in substantial numbers from the rocky shores surrounding the lake.

Capnia promota Frison

Figs. 129–132, 240, map Fig. 270

Capnia promota Frison 1937: 88. Claassen 1940: 95. Hanson 1946: 239. Jewett 1956: 170, 1959: 48, 1960: 146. Illies 1966: 145. Ricker and Scudder 1975: 339. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), Oregon, Benton Co., Corvallis, 23 January 1934, K. Gray; (INHS).

DIAGNOSIS.—This species is distinguished from *C. elongata* by the shorter knob on tergum 7, the presence of a small knob on tergum 8, and the epiproct lacking a distinct swelling on the basal half. This species may be separated from *C. gracilaria* by the laterally expanded epiproct, especially on the distal third. Notes on separating the females are given under *C. gracilaria*.

DISTRIBUTION.—BRITISH COLUMBIA: Vancouver Island, Millstone River, Nanaimo River. OREGON: Benton Co.; Clackamas Co.; Clatsop Co.; Columbia Co.; Coos Co.; Douglas Co.; Jackson Co.; Josephine Co.; Klamath Co.; Lane Co.; Linn Co.; Marion Co.; Multnomah Co.; Polk Co.; Wasco Co.; Washington Co.; Yamhill Co. WASHINGTON: Clark Co.; Grays Harbor Co.; King Co.; Klickitat Co.; Lewis Co.; Wahkiakum Co.; (833). 1 January–26 April.

Mariposa Group

The members of this group, *Capnia giulianii* Nelson & Baumann, *C. inyo* Nelson & Baumann, and *C. mariposa* Nelson & Baumann, are characterized by having a very prominent pair of knobs on tergum 9, which has a groove between them for the reception of the epiproct. Two of the three species have epiproctal horns similar to those of the *decepta* and *barberi* groups; the third species seems to have lost this character secondarily. No other knobs are present on the terga, a feature, or rather a lack of feature, that differentiates them from both of the related groups, *decepta* and *barberi*. Females have a darkened subgenital plate similar to that of members of the *decepta* and *barberi* groups. The females of *C. inyo* and *C. mariposa* are inseparable. The female of *C. giulianii* is unknown, and thus a key is not given below.

DISTRIBUTION.—The group is limited in distribution to the central and southern Sierra Nevada. One species, *C. inyo*, is very common on the eastern slope of the Sierra Nevada from about Mono Lake south. A single specimen of *C. giulianii* has been collected in a stream where *C. inyo* occurs. The remaining species, *C. mariposa*, has been collected at about the same latitude, but a few specimens have been caught at several localities on the west drainages of the Sierra Nevada.

Key to the Males of the Mariposa Group

1. Epiproct short, less than five times as long as high (Figs. 48, 88); dorsal membranous area of epiproct bearing short, dark setae (Figs. 47, 87); lateral horns present on epiproct; epiproct not compoundly curved in lateral view 2

— Epiproct longer, 10 times as long as greatest height laterally (Fig. 68); dorsal membranous area of epiproct white, lacking distinct setae (Fig. 67); lateral horns absent; epiproct compoundly curved in lateral view . . . . *inyo* Nelson & Baumann

2(1). Epiproct with swelling on upper and lower margins at same level, yielding a balanced bird-head–like appearance (Fig. 88); epiproct four times as long as high . . . . *mariposa* Nelson & Baumann

— Epiproct with swelling on upper margin closer to apex than swelling on lower margin, epiproct five times as long as high (Fig. 48) . . . . *giulianii* Nelson & Baumann

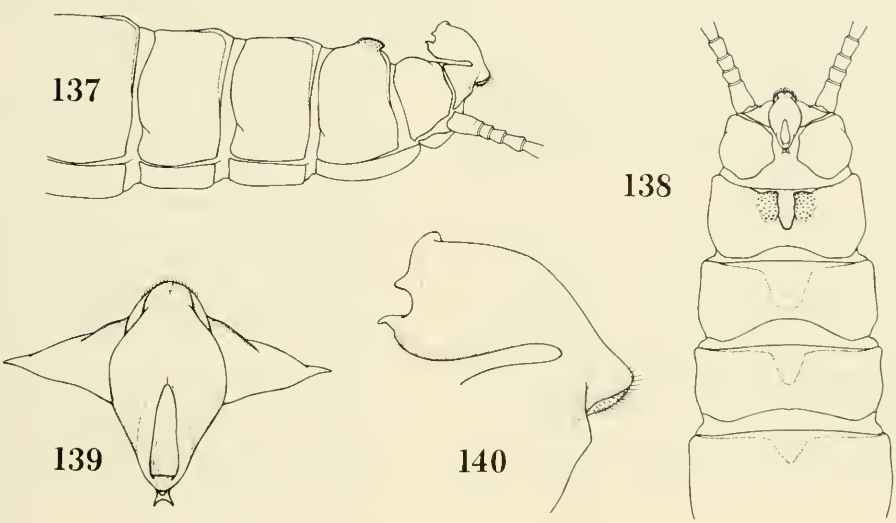
Capnia giulianii Nelson & Baumann

Figs. 45–48, map Fig. 271

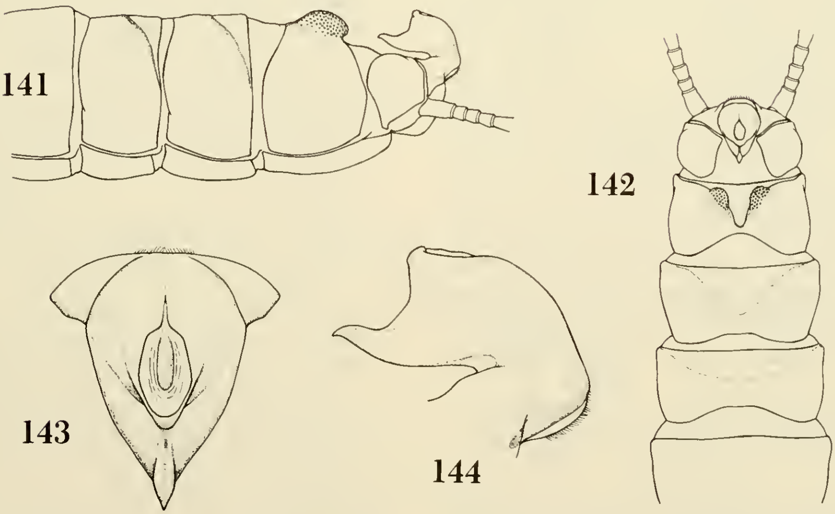
Capnia giulianii Nelson & Baumann 1987c: 499.

HOLOTYPE.—Male, California, Inyo Co., Lone Pine Creek, Whitney Portal Campground, 3 May 1981, R. W. Baumann and J. A. Stanger; (USNM).

DIAGNOSIS.—This species may be distinguished from related forms by the asymmetry of the swellings on the epiproct in lateral view (Fig. 48). The epiproct is not strongly recurved as is that of *C. inyo*.



Capnia regilla



Capnia saratoga

Figs. 137–140. *Capnia regilla* Nelson & Baumann: 137, male terminalia, lateral; 138, male terminalia, dorsal; 139, male epiproct, dorsal; 140, male epiproct, lateral. California, Marin Co., Point Reyes, 14 March 1976, D. G. Denning.

Figs. 141–144. *Capnia saratoga* Nelson & Baumann: 141, male terminalia, lateral; 142, male terminalia, dorsal; 143, male epiproct, dorsal; 144, male epiproct, lateral. California, near Saratoga, 25 February 1940, S. G. Jewett, Jr.

DISTRIBUTION.—CALIFORNIA: Inyo Co.; (1). 3 May.

Capnia inyo Nelson & Baumann

Figs. 65–68, 225, map Fig. 271

Capnia inyo Nelson & Baumann 1987c: 514.

HOLOTYPE.—Male (and female allotype), California, Inyo Co., Independence Creek, Grays Meadow Campground, 25 January 1985, R. W. Baumann and C. R. Nelson; (USNM).

DIAGNOSIS.—This is the only species of North American *Capnia* that has an elongate, compoundly curved epiproct nestled between a pair of knobs on tergum 9 (Figs. 65, 66). The female of this species is very similar and indistinguishable from that of *C. mariposa*, although the *C. mariposa* female is considerably smaller.

DISTRIBUTION.—CALIFORNIA: Inyo Co.; Mono Co.; (700). 7 December–7 May.

Capnia mariposa Nelson & Baumann

Figs. 85–88, 230, map Fig. 271

Capnia mariposa Nelson & Baumann 1987c: 501.

HOLOTYPE.—Male (and female allotype), California, Mariposa Co., Tuolumne River, Highway 120, Tuolumne Meadows Campground, 27 June 1980, R. W. Baumann and J. A. Stanger; (USNM).

DIAGNOSIS.—The male of this species is separated from others in the group, such as *C. inyo* and *C. giulianii*, on the basis of the symmetrical swelling of the midsection of the epiproct and the short epiproct, which does not reach past the anterior margin of tergum 10 in relaxed specimens. The males of this species may also be confused with *C. umpqua* but are distinguished from that species by the presence of lateral horns on the epiproct (Fig. 32).

DISTRIBUTION.—CALIFORNIA: Mariposa Co.; Tuolumne Co.; (9). 18 March–27 June.

Nana Group

The *Capnia nana* group consists of six species, *Capnia glabra* Claassen, *C. licina* Jewett, *C. melia* Frison, *C. nana* Claassen, *C. oregona* Frison, and *C. willametta* Jewett. The group is characterized by having a well-developed tergal knob on segment 8 and a compoundly curved epiproct. The females of the group often have a triangular darkened area on the posterior half of the subgenital plate.

DISTRIBUTION.—Members of this group occur from British Columbia and Alberta south to the central Sierra Nevada and throughout the Rocky Mountains of Idaho and Wyoming south to Utah and Colorado.

Key to the Males of the Nana Group

1. Epiproct with the tip bent to the left of the midline of the specimen (Figs. 51, 115) 2

— Epiproct symmetrical from dorsal view, not bent to the left of the specimen 3

2(1). Epiproct more than seven times as long as high in lateral view, compound curve of epiproct distinct, long, fine hairs present on lower surface of epiproct, sometimes with stout spines present on upper surface of epiproct (Figs. 51, 52) . . . . *glabra* Claassen

— Epiproct less than seven times as long as high, compound curve of epiproct not distinct with lower margin straight or arching toward tip, spines and hairs absent from shaft of epiproct although some short setae may be present (Figs. 115, 116) . . . . *oregona* Frison

3(1). Epiproct narrowing from base to tip in dorsal view, lacking any lateral expansion along length (Fig. 199); compound curve of epiproct indistinct, lower margin of epiproct mostly straight; spines and hairs generally absent from shaft of epiproct (Fig. 200) . . . . *willametta* Jewett

— Epiproct narrowing and then widening, moving from base to apex (Figs. 79, 91, 99, 103); compound curve of epiproct evident in lateral view; spines and hairs present or absent. 4

4(3). Epiproct lacking spines and hairs on shaft (Figs. 100, 104); apex of epiproct not surpassing mid-length of segment 9 in lateral view (Figs. 97, 101), barely reaching level of posterior margin of ninth tergum 9 . . . . *nana* Claassen

— Epiproct with spines and/or hairs (Figs. 80, 91, 92); apex of epiproct surpassing posterior margin of tergum 9 5

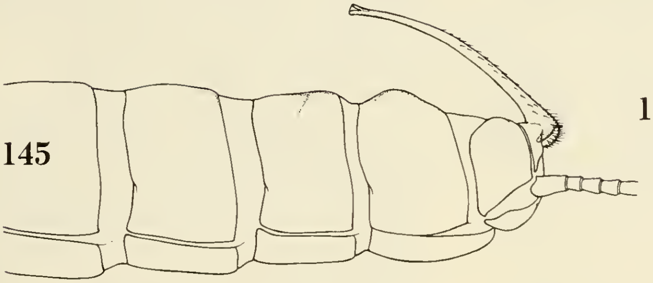
5(4). Epiproct with narrow lateral expansion, greatest width 1.5 times as wide as narrowest in dorsal view (Fig. 79); epiproct with long, fine hairs on lower surface (Fig. 80); upper surface of epiproct microserrulate along lateral margins (Figs. 79, 80); tergal knob on segment 7 well developed, bearing tubercles (Fig. 77) . . . . *licina* Jewett

— Epiproct with wide lateral expansion, greatest width two times as wide as narrowest in dorsal view (Fig. 91); epiproct lacking hairs on lower surface; upper surface of epiproct not microserrulate along lateral margins, but bearing a patch of spines on distal surface of lateral expansion (Fig. 91); tergal knob on segment 7 absent . . . . *melia* Frison

Key to the Females of the Nana Group
(including *C. willametta* unknown)

1. Posterior margin of subgenital plate darkly colored in a narrow band (Figs. 221, 236) 2

145



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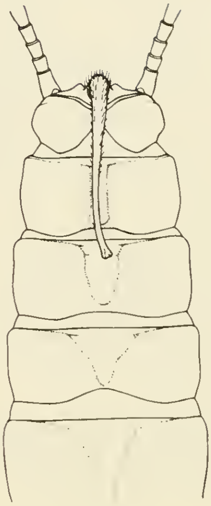

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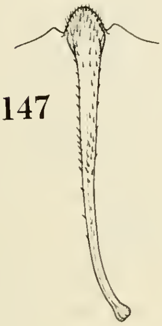

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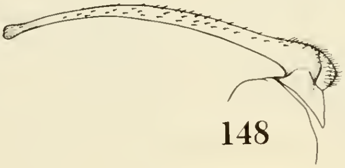
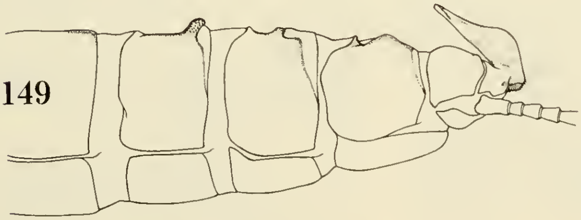


Capnia scobina

149



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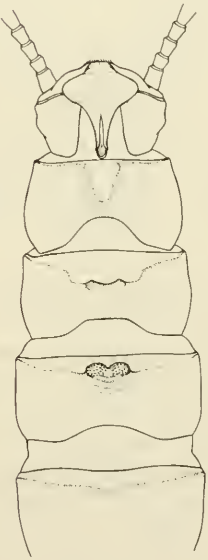

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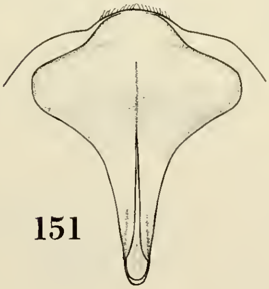

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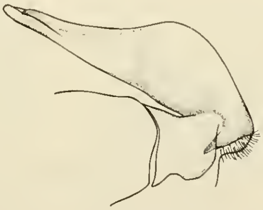


Capnia sequoia

Figs. 145–148. *Capnia scobina* Jewett: 145, male terminalia, lateral; 146, male terminalia, dorsal; 147, male epiproct, dorsal; 148, male epiproct, lateral. California, Nevada Co., Sagehen Creek, 6,300 feet, 15 February 1965, A. L. Sheldon.

Figs. 149–152. *Capnia sequoia* Nelson & Baumann: 149, male terminalia, lateral; 150, male terminalia, dorsal; 151, male epiproct, dorsal; 152, male epiproct, lateral. California, Tuolumne Co., Ackerson Creek, Evergreen Lodge Road, 18 March 1985, R. W. Baumann and C. R. Nelson.

— Posterior margin of subgenital plate either light or with darkly colored area extending anteriorly to cover midline of plate through at least one-third length (Figs. 228, 231, 233, 234) 3

2(1). Subgenital plate light colored except narrow, posterior band of dark sclerotization, any darkening of remainder of plate area internal (Fig. 221); wings hyaline, often shortened . . . . . . *glabra*

— Subgenital plate with a medial darkening extending anteriorly, contrasting with remainder of plate (Fig. 236); wings infuscated, never shortened . . . . *oregona*

3(1). Posterior margin of subgenital plate straight, not produced medially, subgenital plate bearing a triangular dark area with apex medial and arising at about midlength of plate, posterior margin with lateral notches more or less defined (Figs. 233, 234) . . . . *nana*

— Posterior margin of subgenital plate bearing a medial projection, subgenital plate without a well-defined, dark triangle, posterior margin lacking lateral notches (Figs. 228, 231) . . . . *melia* and *licina*

Capnia glabra Claassen

Figs. 49–52, 221, map Fig. 272

Capnia glabra Claassen 1924: 55, 1940: 93. Needham and Claassen 1925: 258. Hanson 1946: 239. Jewett 1956: 170, 1959: 45, 1960: 145, 1966: 102. Gaufin 1964a: 223. Gaufin et al. 1966: 46. Illies 1966: 138. Nebeker and Gaufin 1967a: 419, 1968: 3. Sheldon and Jewett 1967: 4. Stark et al. 1986: 385.

HOLOTYPE.—Male, California, Plumas Co., Sunnyside Mine, 25–26 December 1922, H. S. Barber; (USNM). Female allotype, California, Nevada Co., Sagehen Creek, 6,300 feet, 9 March 1965, A. L. Sheldon; (CAS).

DIAGNOSIS.—The males of this species may be distinguished from most *Capnia* by the epiproct bending asymmetrically to the left. Two other species, *C. oregona* and *C. scobina*, also have an asymmetrical epiproct but are readily separated from *C. scobina* in having shorter epiprocts that end in narrow tips. The females of *C. glabra* have the unique darkly colored posterior margin of the subgenital plate, a character which they share only with *C. oregona*. The females of these two species may be separated by the lack of heavy coloration on the remainder of the plate in *C. glabra*, which is present in *C. oregona*. Additionally, the wings of *C. glabra* are hyaline whereas those of *C. oregona* are fumose.

DISTRIBUTION.—CALIFORNIA: Butte Co.; El Dorado Co.; Mariposa Co.; Nevada Co.; Placer Co.; Plumas Co.; Shasta Co.; Sierra Co.; Siskiyou Co.; Tehama Co.; Tuolumne Co. IDAHO: Adams Co.; Blaine Co.; Boise Co.; Valley Co.; Washington Co. NEVADA: Washoe Co. OREGON: Baker Co.; Jackson Co.; Union Co.; (1340). 9 December–24 June.

Capnia licina Jewett

Figs. 77–80, 228, map Fig. 273

Capnia licina Jewett 1954a: 174, 1959: 46. Illies 1966: 140. Stark et al. 1986: 385. Cannings 1987: 439.

HOLOTYPE.—Male, Oregon, Clackamas Co., small creek at the junction of Highways 36 and 50, 22 April 1948, S. G. Jewett, Jr.; (USNM). Current maps show no junction of Highways 36 and 50 in Clackamas Co. Specimens of this species have been collected at the headwaters of the Salmon River about one-half mile south of the junction of Highways 26 and 35.

DIAGNOSIS.—This species can be separated from others in the group by the epiproct being symmetrical in dorsal view and by the presence of well-developed tergal knobs on segments 7 and 8. This species is also unique in having small serrulations along the dorsolateral margins of the epiproct and fine hairs on the lower surface of the epiproct. The female of this species is indistinguishable from that of *C. melia*.

DISTRIBUTION.—OREGON: Clackamas Co. WASHINGTON: Lewis Co.; Whatcom Co.; (73). 18 February–28 May.

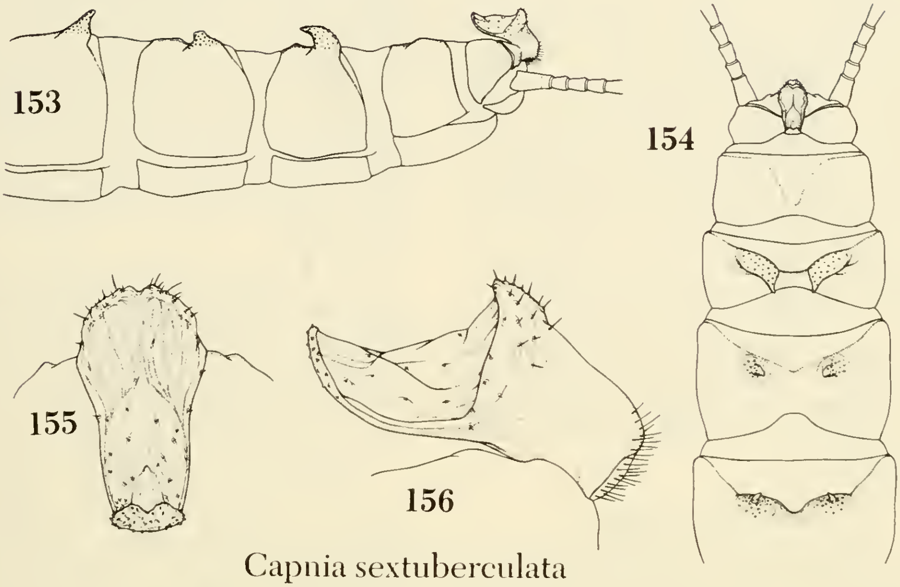
Capnia melia Frison

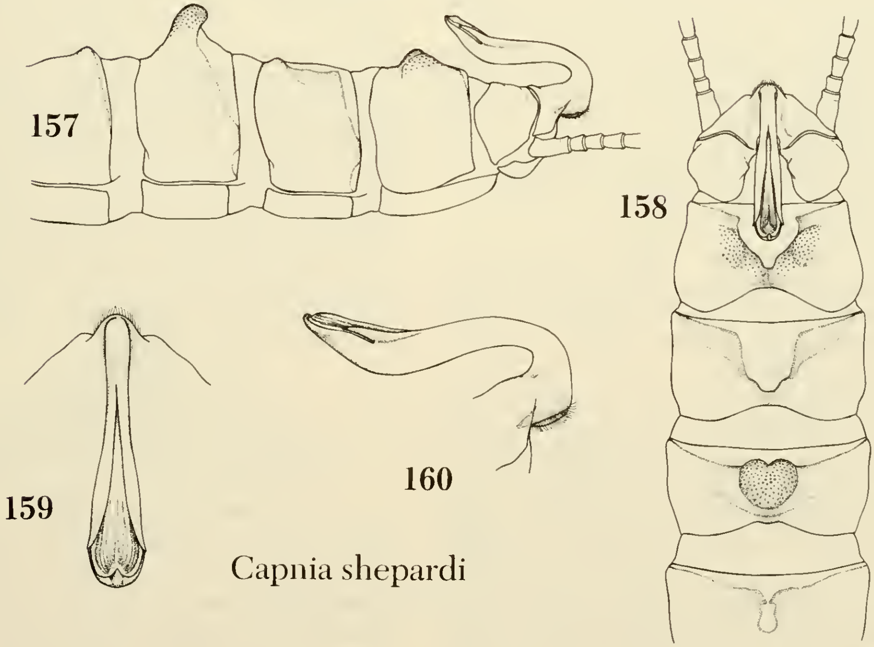
Figs. 89–92, 231, map Fig. 274

Capnia melia Frison 1942: 61. Ricker 1943: 101. Hanson 1946: 239. Jewett 1959: 47. Illies 1966: 141. Ricker and Scudder 1975: 339. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), Oregon, Clackamas Co.; Wildcat Creek, tributary of Sandy River, 3 February 1939, S. G. Jewett, Jr.; (INHS).

DIAGNOSIS.—The male of this species has the epiproct widened and flattened moving from base to tip, then constricting to a pointed apex. The forward-facing portion of the expansion bears small, unsocketed spines that face anteriorly. The broad expansion and spines of the epiproct separate this species from others in the group. The females have a medial projection on the posterior margin of the subgenital plate along with a light triangle of internal sclerotization, which is visible through the plate. The presence of this medial projection should separate this species from others in the group. The plate is a pale color overall, while the often coexisting *C. excavata* has the plate


153
154
155
156
Capnia sextuberculata


157
158
159
160
Capnia shepardi

Figs. 153–156. *Capnia sextuberculata* Jewett: 153, male terminalia, lateral; 154, male terminalia, dorsal; 155, male epiproct, dorsal; 156, male epiproct, lateral. Oregon, Wallowa Co., Lake Creek, junction Lostine River, Lostine Guard Station, 19 May 1977, R. W. Baumann and D. Dunster.

Figs. 157–160. *Capnia shepardi* Nelson & Baumann: 157, male terminalia, lateral; 158, male terminalia, dorsal; 159, male epiproct, dorsal; 160, male epiproct, lateral. California, Mono Co., Lee Vining Creek, Lee Vining Campground, 14 March 1985, R. W. Baumann and C. R. Nelson.

much darkened in addition to having the posterior margin angular.

Distribution.—Alaska: Douglas Island. British Columbia: Cultus Lake; Courtenay; Cypress Bowl Provincial Park; Garibaldi Provincial Park; Grouse Mountain Creek; Keremeos Creek; Lytton, Botanie Lake; Manning Provincial Park; Mount Arrowsmith, small creeks; Queen Charlotte Islands, Graham Island, Massett Inlet, Mamin River; Terrace. California: Siskiyou Co. Oregon: Benton Co.; Clackamas Co.; Clatsop Co.; Columbia Co.; Hood River Co.; Klamath Co.; Lane Co.; Marion Co.; Multnomah Co.; Wasco Co.; Washington Co.; Yamhill Co. Washington: Clark Co.; Cowlitz Co.; King Co.; Kittitas Co.; Klickitat Co.; Pierce Co.; Skamania Co.; Snohomish Co.; (550). 8 January–27 June.

Capnia nana Claassen

Figs. 97–104, 233–234, map Fig. 275

Capnia nana Claassen 1924: 46, 1940: 94. Needham and Claassen 1925: 257. Knowlton and Harmston 1938: 284. Frison 1942: 66. Hanson 1946: 239. Gaufin 1955: 118, 1964a: 223. Jewett 1959: 47, 1966: 104. Gaufin et al. 1966: 47. Illies 1966: 142. Nebeker 1971: 27. Nebeker and Gaufin 1967a: 419, 1967c: 85, 1968: 3. Zwick 1973: 376. Ricker and Scudder 1975: 339. Baumann et al. 1977: 72. Stark et al. 1986: 385.

Capnia nana nana Nebeker & Gaufin 1967b: 239.

Capnia nana wasatchae Nebeker & Gaufin 1967b: 240. Baumann and Gaufin 1971: 108.

Holotype.—Male, Canada, British Columbia, Terrace, March 1923, Mrs. W. W. Hippisley; (CU). Female allotype, Canada, British Columbia, Terrace, 1936, Mrs. M. E. Hippisley; (INHS).

Diagnosis.—The short, straight (dorsal view) epiproct lacking any spines or hairs differentiates the male of this species from all other males in the group. It should be noted that the epiproct expands laterally to a small extent, not, however, as much as does the epiproct of *C. melia*. The female differs from others in the group by often having lateral notches present on the posterior margin of the subgenital plate. The darkened area of the plate extends anteriorly from the posterior margin to form an indistinct triangle. This triangular area of the plate is formed from internal sclerotization that shows through the external sclerotization. *Utacapnia nedia* (Nebeker & Gaufin) superficially resembles *C. nana* but has a heavier base for the epiproct (Nelson and Baumann 1988). The two subspecies are usually distinguished by the southern (*wasatchae*) male specimens having a stouter epiproct (Figs. 103, 104). The females of the two subspecies are not structurally distinguishable except that the northern subspecies (*nana nana*) has a slightly more delicate coloration of the subgenital plate. As noted by Nebeker and Gaufin (1967c), this species exhibits a wide variation in wing length throughout its range.

Distribution.—Alaska: Dewey Creek. Alberta: Louise Creek, Lake Louise. British Columbia: Ashnola River; Lytton, Botanie Lake; Manning Provincial Park; McLeod Hill; Paulson Summit near Castlegar; Penticton, Ellis Creek; Shingle Creek; Terrace; Wells Gray Provincial Park. Colorado: Archuleta Co.; Conejos Co.; Gunnison Co. Idaho: Ada Co.; Adams Co.; Bannock Co.; Blaine Co.; Boise Co.; Bonneville Co.; Caribou Co.; Clearwater Co.; Custer Co.; Franklin Co.; Fremont Co.; Idaho Co.; Kootenai Co.; Latah Co.; Valley Co.; Washington Co. Montana: Cascade Co.; Flathead Co.; Gallatin Co.; Glacier Co.; Lake Co.; Missoula Co.; Ravalli Co. Oregon: Baker Co.; Clackamas Co.; Klamath Co.; Linn Co.; Union Co.; Wallowa Co.; Washington Co.; Wheeler Co. Utah: Box Elder Co.; Cache Co.; Carbon Co.; Davis Co.; Emery Co.; Salt Lake Co.; Summit Co.; Tooele Co.; Utah Co.; Wasatch Co.; Weber Co. Washington: Klickitat Co.; Whatcom Co. Yukon Territory: Kluane, Boutellier Creek tributary; Whitehorse, Wolf Creek; (3900). 1 November–4 June.

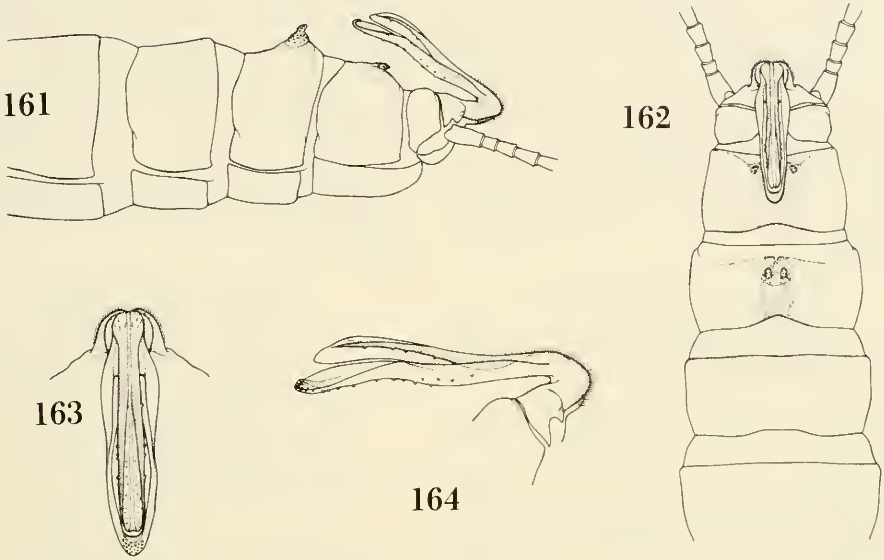
Capnia oregona Frison

Figs. 113–116, 236, map Fig. 273

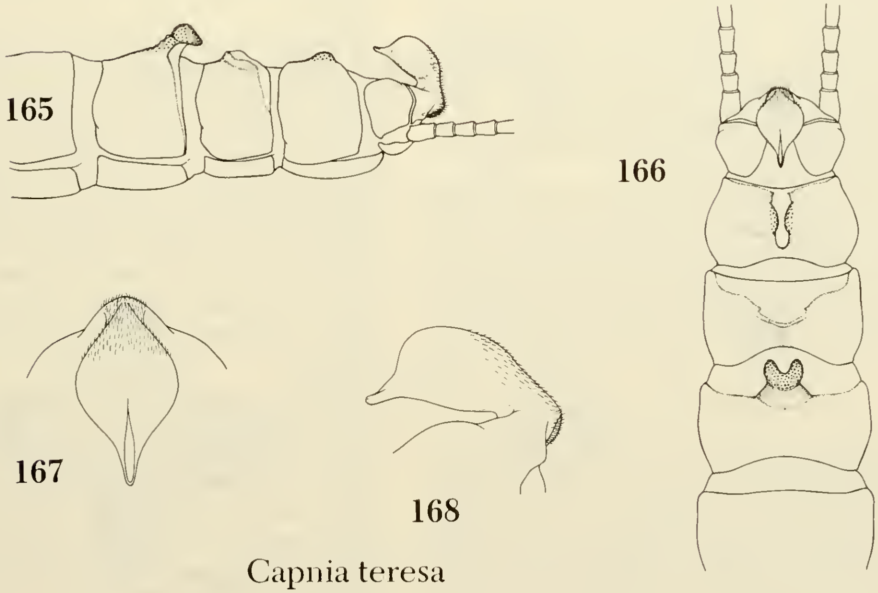
Capnia oregona Frison 1942: 63. Hanson 1946: 239. Jewett 1954a: 175, 1959: 47. Illies 1966: 144. Stark et al. 1986: 385.

Holotype.—Male, Oregon, Benton Co., Muddy Creek, 14 miles south of Corvallis, 10 February 1938, S. G. Jewett, Jr.; (INHS). Female allotype, same data as holotype, described later by Jewett (1954a); (CAS).

Diagnosis.—The male of this species has an epiproct which bends to the left asymmetrically and is sharply attenuated at the tip. *Capnia glabra* and *C. scobina* are similarly asymmetrical, but *C. glabra* has a somewhat longer epiproct that is blunt at the tip and *C. scobina* has a much longer epiproct, armed with dorsolateral spines and blunt at the tip.



Capnia spinulosa



Capnia teresa

Figs. 161–164. *Capnia spinulosa* Claassen: 161, male terminalia, lateral; 162, male terminalia, dorsal; 163, male epiproct, dorsal; 164, male epiproct, lateral. California, Los Angeles Co., San Gabriel Mountains, 0.5 miles northeast of Camp Valcrest, 24 April 1977, C. L. Hogue.

Figs. 165–168. *Capnia teresa* Claassen: 165, male terminalia, lateral; 166, male terminalia, dorsal; 167, male epiproct, dorsal; 168, male epiproct, lateral. California, San Bernardino Co., San Antonio Creek at Mount Baldy Village, 22 January 1985, R. W. Baumann and C. R. Nelson.

The female of *C. oregona* has a subgenital plate similar to that of other females in the group but can be distinguished from them by the somewhat larger body size and by the distinctly gray fumose wing color in fresh specimens, which fades to a reddish brown tinge in older, preserved specimens.

DISTRIBUTION.—OREGON: Benton Co.; Clackamas Co.; Clatsop Co.; Columbia Co.; Hood River Co.; Linn Co.; (68). 10 February–20 July.

Capnia willametta Jewett

Figs. 197–200, map Fig. 272

Capnia willametta Jewett 1955: 147, 1959: 49. Illies 1966: 150. Stark et al. 1986: 385.

HOLOTYPE.—Male, Oregon, Benton Co.; Dixon Creek, 19 January 1935, R. W. Prentiss; (INHS).

DIAGNOSIS.—The male of this species has an epiproct similar to that of *C. licina* but much flatter in lateral view. The compound curving of the epiproct is not as pronounced in *C. willametta* as in *C. licina*. The epiproct of *C. willametta* is not expanded laterally in dorsal view as in *C. licina*, nor does it bear any spines or hairs. The female is unknown. The enigmatic species *C. erecta* Jewett may be conspecific with *C. willametta*.

DISTRIBUTION.—Oregon, Benton Co.; (3). 23 January.

NOTES.—Several attempts have been made by the authors and helpful individuals to recollect this rare species. All attempts to collect fresh specimens have failed. The holotype of this species may be an aberrant specimen of *C. erecta*, which it closely resembles.

Nearctica Group

This group of species has two members in the Nearctic region, *C. nearctica* Banks and *C. valhalla* Nelson & Baumann. Several other representatives of this group are known from the Palearctic region, including a species endemic to Lake Baikal. The inclusion of this group in *Capnia* is problematic. It could be placed in a different genus, and several have been proposed for the Palearctic species. It is beyond the scope of this article to treat the generic problems of the family Capniidae on a worldwide scale. Therefore, these species are tentatively left in *Capnia*.

The members of this group are characterized by having the epiproct consisting of two limbs that are appressed basally, with the distal portion of the lower limb separating from the upper and arching over the abdomen. The only other North American "*Capnia*" (broad sense) with a two-limbed epiproct is *Capnia spinulosa*, which differs from *C. nearctica* and *C. valhalla* in having the two limbs closely appressed throughout the length of the epiproct. Males and females can be identified using the group key at the beginning of this article.

Capnia nearctica Banks

Figs. 105–108, 235, map Fig. 276

Capnia nearctica Banks 1918: 3. Needham and Claassen 1925: 264. Claassen 1940: 94. Ricker 1944: 178, 1954: 37, 1964: 62. Hanson 1946: 239. Weber 1950: 175. Illies 1966: 142. Ricker and Scudder 1975: 339. Stark et al. 1986: 385.

Capnia hantzchi Ricker 1938b: 173, 1944: 178. Claassen 1940: 93. Hanson 1946: 239.

HOLOTYPE.—Male, Bernard Harbour, Northwest Territories, Canadian Arctic Expedition, 25 June 1915, F. Johansen. Deposited in CNC but apparently lost, not examined by authors.

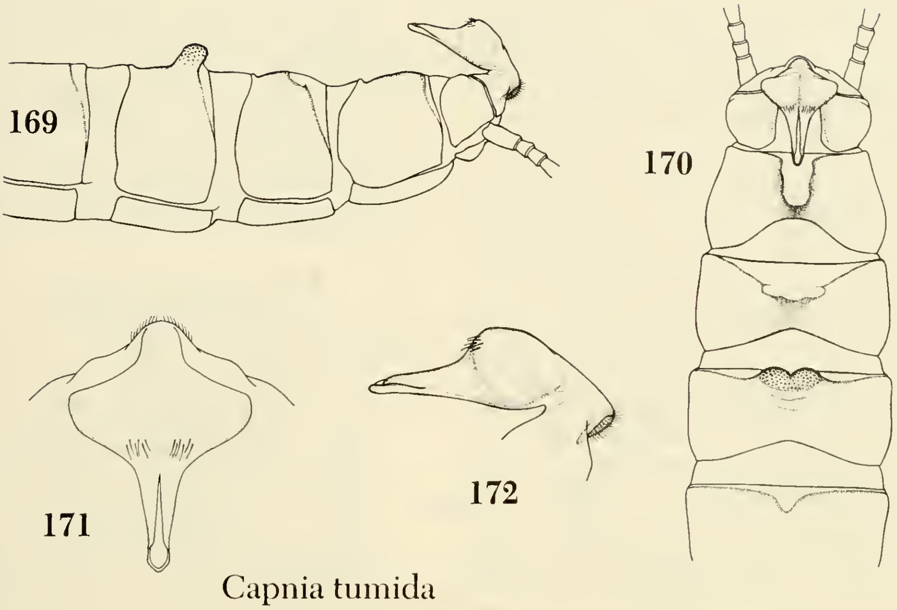
DIAGNOSIS.—The male of this species has the epiproct consisting of two limbs tightly appressed to each other throughout a major portion of their length. The distal third of the lower limb arches above the abdomen. It is closely related to *C. valhalla*, and diagnosing features are listed under that species. The females have a small, darkened subgenital plate that somewhat resembles that of several *Utacapnia* species. This resemblance may indicate a phylogenetic relationship between these taxa.

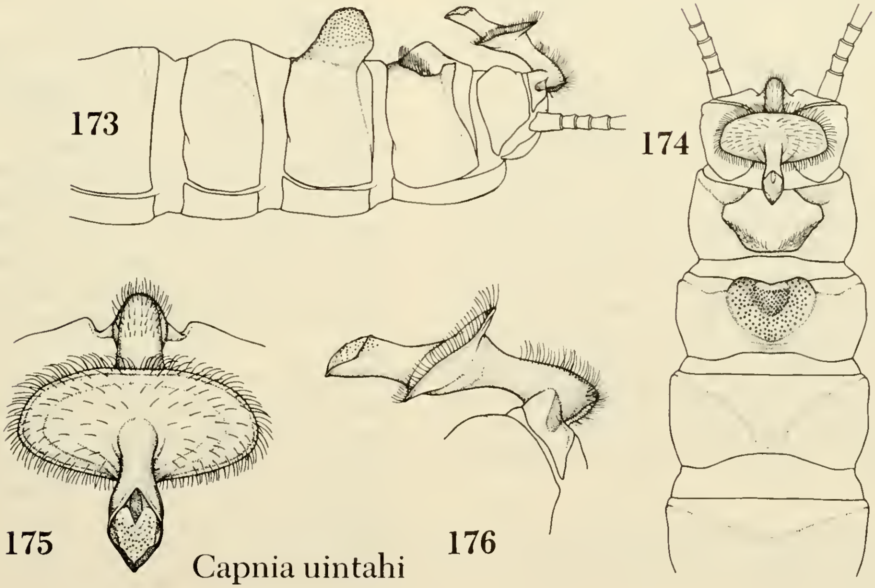
DISTRIBUTION.—ALASKA: Anaktuvuk Pass; Joolik Lake; Kikitaliorak Lake; Meade River; Noatak River, Feniak Lake; Oilspill Lake. BRITISH COLUMBIA: Atlin. NORTHWEST TERRITORIES: Keewatin District: Armark River, 30 miles upriver; Baffin Island; Baker Lake, Chesterfield Inlet; Great Slave Lake; Nettilling Lake. Mackenzie District: Arlone Lake; Bernard Harbour; Coppermine River mouth; Great Bear Lake, Echo Bay (Port Radium); Lake MacAlpine. YUKON TERRITORY: Alligator Lake; Horseshoe Bay Campground; Ogilvie Mountains. (63). 3 June–26 July.

Capnia valhalla Nelson & Baumann

Figs. 185–188, 254, map Fig. 276

Capnia valhalla Nelson & Baumann 1987c: 510.


169
170
171
172
Capnia tumida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176
Capnia uintahi

Figs. 169–172. *Capnia tumida* Claassen: 169, male terminalia, lateral; 170, male terminalia, dorsal; 171, male epiproct, dorsal; 172, male epiproct, lateral. California, Plumas Co., Mosquito Creek at junction North Fork Feather River, 14 February 1985, R. W. Baumann and C. R. Nelson.

Figs. 173–176. *Capnia uintahi* Gaufin: 173, male terminalia, lateral; 174, male terminalia, dorsal; 175, male epiproct, dorsal; 176, male epiproct, lateral. Utah, Wasatch Co., Provo River, Stewarts Ranch, 2 March 1949, A. R. Gaufin.

HOLOTYPE.—Male, California, San Diego Co., Palomar Mountain, Fry Creek, Fry Creek Campground, road S–6, 18 January 1985, R. W. Baumann and C. R. Nelson; (USNM). Female allotype, Los Angeles Co., San Gabriel Mountains, 0.5 miles east of Horseflat Road, 6 March 1977, C. L. Hogue, no. 229; (LACM).

DIAGNOSIS.—The male of this species is distinct among *Capnia* in having a two-limbed epiproct. This species can be separated from *C. spinulosa* by the widely separated limbs of the epiproct, which arch freely over part of the epiproctal length. This species is most closely related to *C. nearctica*, from which it may be distinguished by the basal narrowing of the epiproct and the longer arched portion of the lower limb in *C. valhalla*. These two species may be further separated by the more extensive tergal knobs in *C. valhalla*. The female can be separated from all others in the genus except *C. uintahi* by the notch on the anterior margin of the subgenital plate and from *C. uintahi* by the darkened triangle on the plate.

DISTRIBUTION.—CALIFORNIA: Los Angeles Co.; San Diego Co.; (12). 18 January–31 March.

Vernalis Group

The *C. vernalis* group consists of three species, *C. confusa* Claassen, *C. lineata* Hanson, and *C. vernalis* Newport. The members of the group are united by the synapomorphic character of a medial bridge or bridge vestige between the abdominal sternites 7 and 8 of the female. The epiproct of the male is produced as a simple tube with little modification. The abdominal tergites of the males are without knobs. All three species emerge late in the seasonal succession of capniids, with *C. confusa* generally being the last capniid species to disappear during the spring and summer months.

Key to the Males of the Vernalis Group

1. Epiproct of uniform width through length when viewed laterally 2

— Epiproct narrowed on distal third to about one-half width at base (Fig. 196) .... *vernalis* Newport

2(1). Epiproct reaching anterior margin of tergum 9 (Fig. 82), brachypterous, in streams of Latah County, Idaho .... *lineata* Hanson

— Epiproct not reaching anterior margin of tergum 9 (Fig. 25), wings usually long (somewhat shortened in lake-dwelling forms), widespread in distribution .... *confusa* Claassen

Key to the Females of the Vernalis Group

1. Medial bridge between sternites 7 and 8 complete (Fig. 256) .... *vernalis*

— Medial bridge between sternites 7 and 8 interrupted 2

2(1). Medial bridge reduced to two small, irregular sclerites imbedded in intersegmental membrane (Fig. 229) .... *lineata*

— Medial bridge represented by hind margin of sternite 7 projecting posteriorly into intersegmental membrane, but separated from sternite 8 by membrane (Fig. 216) .... *confusa*

Capnia confusa Claassen

Figs. 25–28, 216, map Fig. 277

Capnia nivalis Neave 1929: 163 (preoccupied by Ueno 1929: 143).

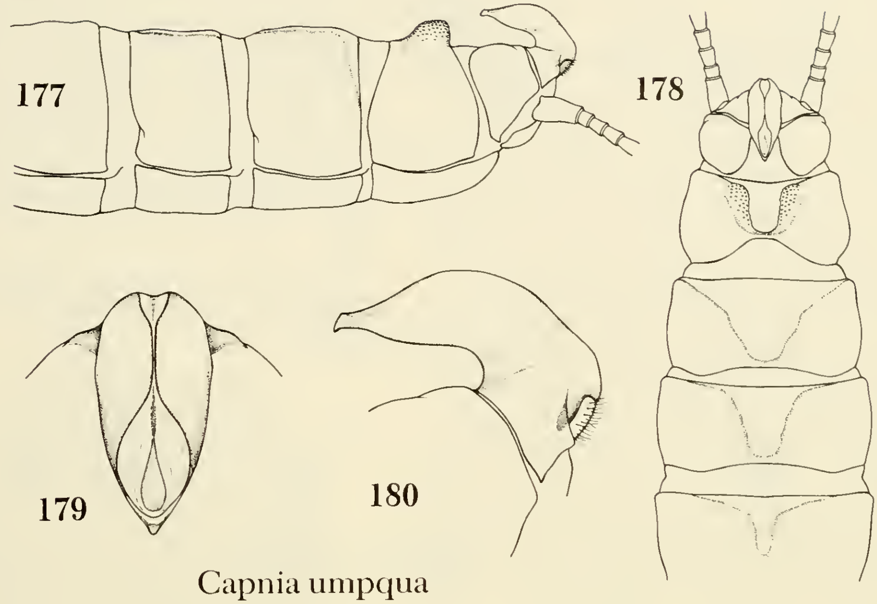
Capnia confusa Claassen 1936: 623, 1940: 92. Ricker 1943: 102, 1964: 61. Hanson 1946: 238. Weber 1950: 175. Gaufin 1955: 118, 1964a: 223. Jewett 1959: 43, 1962: 15. Gaufin et al. 1966: 45, 1972: 66. Illies 1966: 135. Nebeker and Gaufin 1966: 42, 1967a: 419, 1968: 2. Hitchcock 1969: 314. Newell 1970: 50. Baumann and Gaufin 1971: 108. Nebeker 1971: 27. Radford and Hartland-Rowe 1971: 660. Zwick 1973: 372. Ricker and Scudder 1975: 338. Baumann et al. 1977: 68. Dosdall and Lemkuhl 1979: 28. Donald and Anderson 1980: 756. Flannagan and Flannagan 1982: 23. Jacobi and Baumann 1983: 586. Donald and Patriquin 1983: 921. Stark et al. 1986: 385.

Capnia ligatula Hanson 1943a: 85. Illies 1966: 140.

HOLOTYPE.—Male (and female allotype), Maligne Lake, Jasper National Park, Alberta, no repository listed, not examined.

DIAGNOSIS.—This species is separated from related species on the basis of the somewhat shorter epiproct of the male, which is not narrowed toward the apex. The females are unique in having a medial projection of dark sclerotization on the posterior margin of sternum 7.

DISTRIBUTION.—This is probably the most widespread member of the genus in North America. ALASKA: Anuktuvuk; Chena River, Monument Creek; Chugach Mountains; Echootka River; Katmai National Park; Ketchikan, 15 miles north; Kodiak Island; Ugashik Lake. ALBERTA: Jasper National Park, Maligne Lake; Athabasca River; Banff National Park, Spray River. ARIZONA: Apache Co.; Graham Co. BRITISH COLUMBIA: Atlin; Bromley Provincial Park; Charlie Lake; Cheakamus River; Cultus Lake; Elk River; Fraser River, Agassiz; Glacier Park; Keremeos Creek; Lake Lisadele; Meadow Creek Highway 3; Moosehorn Lake; Moyie River below Cultus Lake; Pine River, Lemoray;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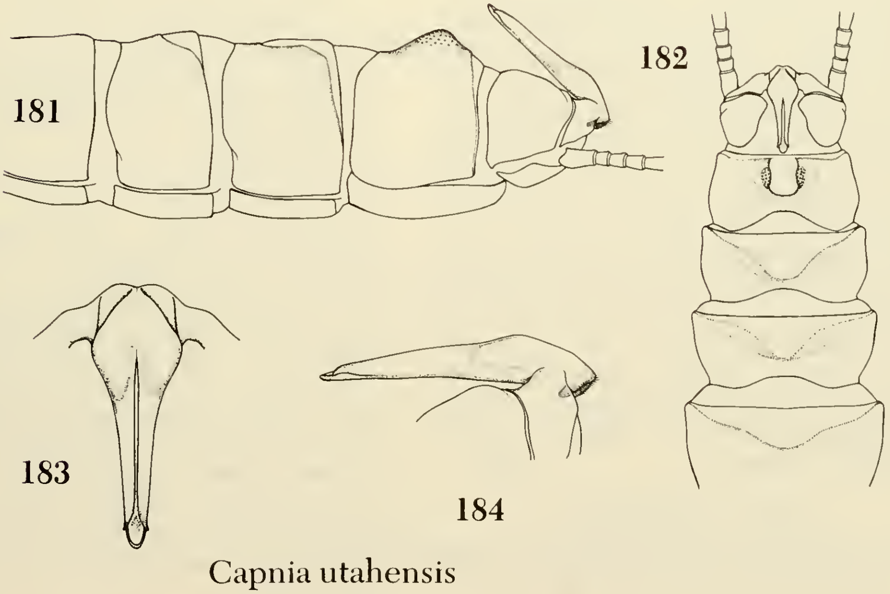
Capnia umpqua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184
Capnia utahensis

Figs. 177–180. *Capnia umpqua* Frison: 177, male terminalia, lateral; 178, male terminalia, dorsal; 179, male epiproct, dorsal; 180, male epiproct, lateral. California, Shasta Co., Sulphur Creek, Castle Crags State Park, 16 February 1985, R. W. Baumann and C. R. Nelson.

Figs. 181–184. *Capnia utahensis* Gaufin & Jewett: 181, male terminalia, lateral; 182, male terminalia, dorsal; 183, male epiproct, dorsal; 184, male epiproct, lateral. Utah, Beaver Co., South Creek, 0.5 mile south of Beaver, 21 February 1965, A. V. Nebeker.

Salmo, southwest on Highway 3; Similkameen River; Stoney Creek; Sumas River; Vedder Crossing. CALIFORNIA: Alpine Co.; Mono Co. COLORADO: Boulder Co.; Chaffee Co.; Clear Creek Co.; Conejos Co.; Dolores Co.; Eagle Co.; El Paso Co.; Garfield Co.; Grande Co.; Gunnison Co.; Hinsdale Co.; Huerfano Co.; Jackson Co.; Jefferson Co.; La Plata Co.; Larimer Co.; Montezuma Co.; Ouray Co.; Pitkin Co.; Routt Co.; San Miguel Co.; Summit Co.; Teller Co. IDAHO: Adams Co.; Bannock Co.; Bear Lake Co.; Benewah Co.; Blaine Co.; Boise Co.; Bonneville Co.; Butte Co.; Custer Co.; Franklin Co.; Fremont Co.; Idaho Co.; Latah Co.; Lemhi Co.; Shoshone Co.; Twin Falls Co.; Valley Co. MANITOBA: Crawford Creek; Little Ochre River; Neepawa Creek; South Duck River. MONTANA: Cascade Co.; Flathead Co.; Gallatin Co.; Glacier Co.; Granite Co.; Lake Co.; Lincoln Co.; Mineral Co.; Missoula Co.; Park Co.; Ravalli Co.; Sanders Co. NEVADA: White Pine Co. NEW MEXICO: Colfax Co.; Lincoln Co.; Rio Arriba Co.; Sandoval Co.; San Miguel Co.; Taos Co. OREGON: Baker Co.; Union Co.; Wallowa Co. SOUTH DAKOTA: Lawrence Co. UTAH: Beaver Co.; Box Elder Co.; Cache Co.; Carbon Co.; Daggett Co.; Emery Co.; Garfield Co.; Grand Co.; Iron Co.; Millard Co.; Morgan Co.; Piute Co.; Salt Lake Co.; San Juan Co.; Sanpete Co.; Sevier Co.; Summit Co.; Uintah Co.; Utah Co.; Wasatch Co.; Washington Co., Weber Co. WASHINGTON: Clallam Co.; Jefferson Co.; Kittitas Co.; Klickitat Co.; Pierce Co. WYOMING: Fremont Co.; Lincoln Co.; Park Co.; Platte Co.; Sublette Co.; Teton Co. YUKON TERRITORY: Alaska Highway, Horseshoe Bay Campground; Dempster Highway, km 142; North Fork Pass, Ogilvie Mountains; (3300). 4 January–6 August.

Capnia lineata Hanson

Figs. 81–84, 229, map Fig. 278

Capnia lineata Hanson 1943: 85, 1946: 239. Jewett 1959: 47. Illies 1966: 140. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), Idaho, Latah Co., Troy, 22 April 1911; (Hanson Collection; USNM; on slide).

DIAGNOSIS.—The male of this species most closely resembles that of *C. confusa*; the two are distinguished on the basis of the relatively longer epiproct of *C. lineata*. The females of these two species are separated by the presence of vestiges of a sclerotized bridge between sternites 7 and 8 of *C. lineata*, which are represented by variably shaped small sclerites imbedded in the medial membrane between the two sterna as opposed to the posteriorly projecting medial margin of sternum 7 in *C. confusa*. All examined male specimens of *C. lineata* have been short-winged, while those of the other two species in the group are longer winged. This species is often collected with *C. zukeli* Hanson and *Capnura venosa* Banks.

DISTRIBUTION.—IDAHO: Latah Co.; several creeks in the Troy area; (125). 24 February–28 June.

Capnia vernalis Newport

Figs. 193–196, 256, map Fig. 278

Capnia vernalis Newport 1848: 388, 1851: 451. Sharp 1895: 395. Needham and Claassen 1925: 256. Claassen 1931: 109, 1940: 95. Ricker 1938: 135, 1944: 178, 1946:5, 1964: 55. Essig 1942: 147. Harden and Mickel 1952: 24. Gaufin 1956: 323 (*Paracapnia?*). Brinck 1958: 53. Illies 1966: 149. Nebeker and Gaufin 1967b: 419, 1968: 3. Ricker et al. 1968: 1110. Kimmins 1970: 352. Zwick 1973: 380. Ricker and Scudder 1975: 339. Baumann et al. 1977: 74. Stark et al. 1986: 385.

Nemoura tenuis Walker 1852: 182.

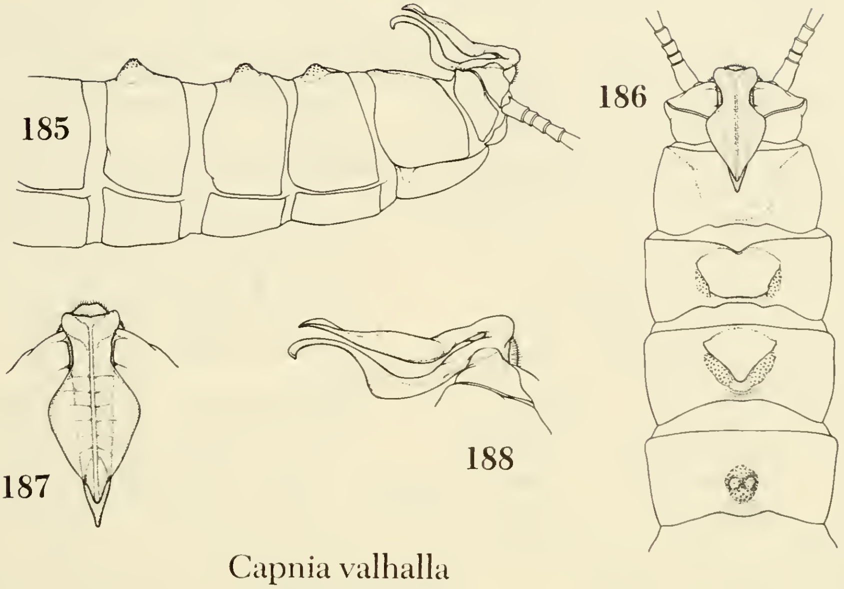
Capnia limata Frison 1944: 155. Hanson 1946: 239. Gaufin 1964a: 223. Ricker 1964: 55. Gaufin et al. 1966: 47. Illies 1966: 140. Nebeker and Gaufin 1967a: 419, 1967b: 247, 1968: 3. Newell 1970: 50. Zwick 1973: 374.

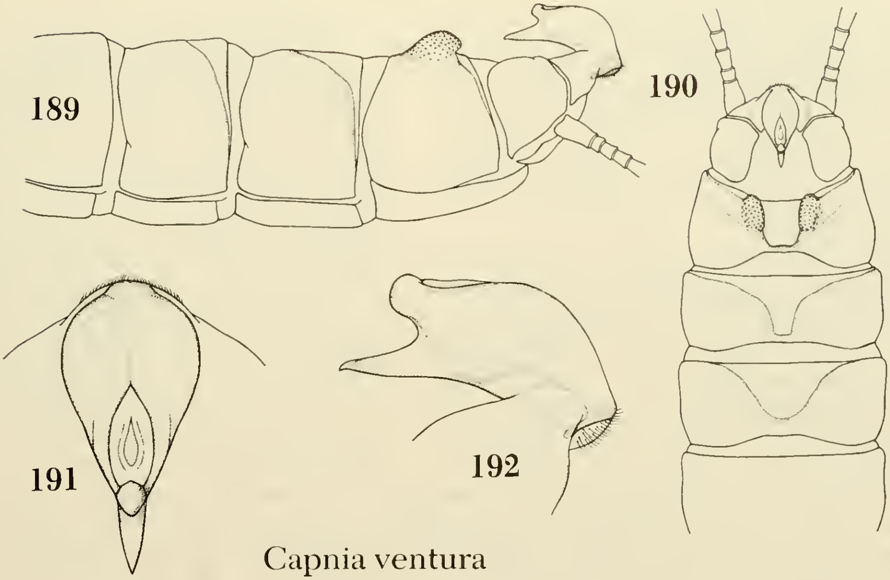
Capnia limita [sic] Gaufin 1955: 118. Knight and Gaufin 1966: 669, 1967: 348.

HOLOTYPE:.—Male, Canada, Ontario, Albany River; (British Museum).

DIAGNOSIS.—Males of this species are readily distinguished from the other two species in the group by the narrowing on the distal third of the epiproct. Females of this species have a narrow bridge of sclerotization joining sternites 7 and 8; vestiges of this bridge are present in *C. lineata* and *C. confusa* but never to the extent that the sclerotization crosses the intersegmental membrane. *Capnia vernalis* has the most eastern distribution for species in North America.

DISTRIBUTION.—ALASKA: West Fork Chena River. ALBERTA: Banff National Park, Athabasca River; Edmonton; Lethbridge; McLeod River; Medicine Hat; Oldman River; Saskatchewan River. BRITISH COLUMBIA: Fraser River, Agassiz. COLORADO: Arapahoe Co.; Archuleta Co.; Chaffee Co.; Conejos Co.; Douglas Co.; Grand Co.; Gunnison Co.;





Figs. 185–188. *Capnia valhalla* Nelson & Baumann: 185, male terminalia, lateral; 186, male terminalia, dorsal; 187, male epiproct, dorsal; 188, male epiproct, lateral. California, San Diego Co., Palomar Mountain, Fry Creek, Road S–6, Fry Creek Campground, 18 January 1985, R. W. Baumann and C. R. Nelson.

Figs. 189–192. *Capnia ventura* Nelson & Baumann: 189, male terminalia, lateral; 190, male terminalia, dorsal; 191, male epiproct, dorsal; 192, male epiproct, lateral. California, Ventura Co., Bear Creek, Wheeler Gorge Campground north of Ojai, 23 January 1985, R. W. Baumann and C. R. Nelson.

Jackson Co.; Jefferson Co.; Moffat Co.; Montrose Co.; Pueblo Co.; Routt Co. IDAHO: Benewah Co.; Blaine Co.; Cassia Co.; Power Co. MINNESOTA: Lake Co., Stewart River; St. Louis Co., Duluth. MONTANA: Broadwater Co.; Cascade Co.; Custer Co.; Gallatin Co.; Madison Co. NEVADA: Elko Co. NEWFOUNDLAND: Anatalak Bay, Nain. NEW MEXICO: Colfax Co.; Rio Arriba Co. NORTHWEST TERRITORIES: Escarpment Creek at Mackenzie Highway. ONTARIO: Hudson Bay, Winisk River at Winisk. OREGON: Harney Co.; Malheur Co. QUEBEC: Bonaventure Co., Charlevoix Co., Chicoutimi Co., Gaspe Co., Lake St. John Co., Matane Co., Montmagny Co., Montmorency Co., Portneuf Co., Saguenay Co., Ungava Co. SASKATCHEWAN: Saskatoon. UTAH: Box Elder Co.; Cache Co.; Duchesne Co.; Garfield Co.; Grand Co.; Sevier Co.; Summit Co.; Uintah Co.; Utah Co. WYOMING: Albany Co.; Carbon Co.; Lincoln Co.; Platte Co.; Sublette Co.; Uintah Co.; (520). 7 February–8 July.

Species of Uncertain Group Status

Capnia scobina Jewett

Figs. 145–148, 244, map Fig. 279

Capnia scobina Jewett 1966: 105. Nebeker and Gaufin 1967a: 418. Sheldon and Jewett 1967: 4. Zwick 1973: 378. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), California, Nevada Co., Sagehen Creek, 6,300 feet elevation, 15 February 1965, A. L. Sheldon; (CAS).

DIAGNOSIS.—The asymmetrical bending of the male epiproct in dorsal view separates this species from all other North American *Capnia* except *C. glabra* and *C. oregona*. This species may be distinguished from the latter two by the much longer and thinner epiproct, which arches simply over the dorsum of the abdomen rather than having a compound curve along its length. The subgenital plate of the female is simple and not heavily sclerotized. The posterior margin of the subgenital plate is recessed anterior to the end of the segment.

DISTRIBUTION.—CALIFORNIA: Alpine Co.; El Dorado Co.; Inyo Co.; Mariposa Co.; Nevada Co.; Placer Co.; Sierra Co. NEVADA: Washoe Co.; (3585). 28 December–13 May.

Capnia sextuberculata Jewett

Figs. 153–156, 246, map Fig. 279

Capnia sextuberculata Jewett 1954: 547, 1959: 48. Illies 1966: 146. Nebeker and Gaufin 1967a: 418, 1967b: 239, 1968: 3. Newell 1970: 50. Baumann et al. 1977: 73. Stark et al. 1986: 385.

HOLOTYPE.—Male, Oregon, Baker Co., Spring Creek, tributary of Powder River, 23 March 1952, J. H. Baker; (CAS).

DIAGNOSIS.—The three pairs of pointed tergal knobs present on the abdomen distinguish this species from all others in the genus. The extremely short and membranous epiproct is also unique. This species is very small and the males are brachypterous. The small size of the female, along with the subgenital plate that has an hourglass shape of sclerotization, should differentiate this species from all others.

DISTRIBUTION.—ALBERTA: Banff National Park. BRITISH COLUMBIA: Lytton, Botanie Lake. IDAHO: Adams Co.; Boise Co.; Caribou Co.; Valley Co. MONTANA: Cascade Co.; Flathead Co.; Gallatin Co.; Lake Co.; Missoula Co.; Stillwater Co. OREGON: Baker Co.; Wallowa Co. WASHINGTON: Chelan Co.; Pierce Co.; Whatcom Co. WYOMING: Teton Co.; (300). 6 March–9 June.

Capnia spinulosa Claassen

Figs. 161–164, 248, map Fig. 279

Capnia spinulosa Claassen 1937: 80, 1940: 95. Hanson 1946: 239. Jewett 1956: 169, 1960: 146. Illies 1966: 147. Stark et al. 1986: 385.

HOLOTYPE.—Male (and female allotype), southern California; (CU).

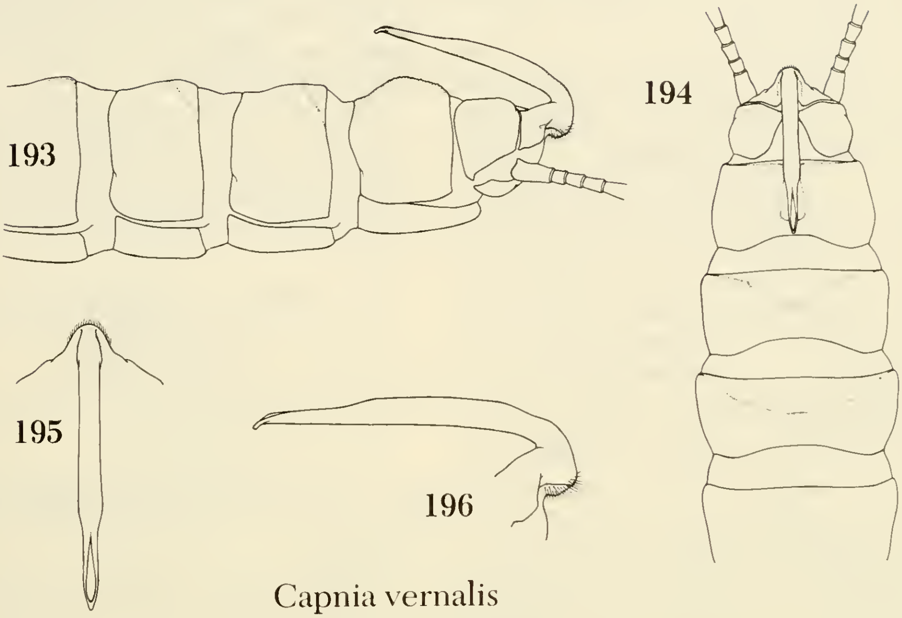
DIAGNOSIS.—The presence of paired tergal projections and the two-limbed epiproct will separate this species from most others in the genus *Capnia*. The females may be distinguished from others in the genus on the basis of the narrow, dark, sclerotized subgenital plate that extends from the anterior margin to the posterior margin of sternum 8.

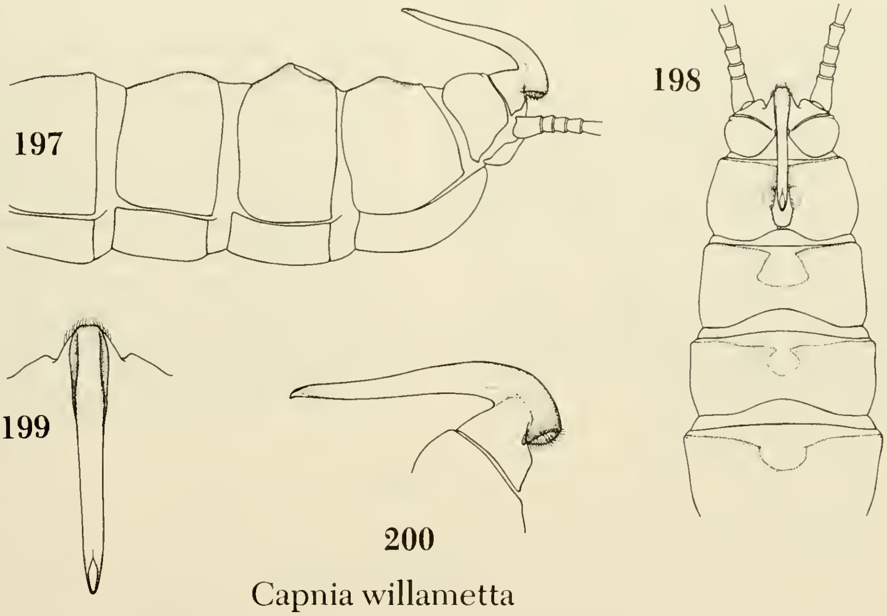
DISTRIBUTION.—CALIFORNIA: Los Angeles Co.; San Gabriel Mountains; 0.5 miles northeast of Camp Valcrest; San Gabriel Mountains; 0.5 miles east of Horseflats; Placerita Canyon Creek, Placerita Canyon State Park. Riverside Co., P. L. Boyd Desert Research Center, 3.5 miles south of Palm Desert; (25). 21 January–24 April.

Capnia zukeli Hanson

Figs. 205–208, 258, map Fig. 279

Capnia zukeli Hanson 1943a: 86. Jewett 1959: 49. Illies 1966: 151. Baumann et al. 1977: 72 (in part). Stark et al. 1986: 385.


193
194
195
196
Capnia vernalis


197
198
199
200
Capnia willametta

Figs. 193–196. *Capnia vernalis* Newport: 193, male terminalia, lateral; 194, male terminalia, dorsal; 195, male epiproct, dorsal; 196, male epiproct, lateral. Montana, Broadwater Co., Missouri River, Toston, 28 March 1952, R. Hays.

Figs. 197–200. *Capnia willametta* Jewett: 197, male terminalia, lateral; 198, male terminalia, dorsal; 199, male epiproct, dorsal; 200, male epiproct, lateral. Oregon, Benton Co., Dixon Creek, Corvallis, 23 January 1935, R. W. Prentiss.

HOLOTYPE.—Male (and female allotype), Idaho, Latah Co., Moscow, 2,560 feet, 2 April 1938, Zukel; (USNM).

DIAGNOSIS.—The extremely long epiproct (30 times as long as wide), the absence of tergal knobs, and brachyptery distinguish this species from all others in the genus. Baumann et al. (1977) synonymized this species with *C. lineata*, based on limited material. Further collecting and careful examination of the types showed two distinct forms of both males and females in the material from Latah Co., Idaho. Each of the two species names available (*C. lineata* and *C. zukeli*) is referable to one of these forms. The illustrations given in the original descriptions are representative of each of the species. The descriptions and figures given for the female of this species and *C. lineata* by Hanson (1943a) are ambiguous and fail to separate the females of the two species. Hanson most likely described the females of both species from material of one of the species, probably *C. zukeli*. Proper associations have now been made using material collected in the absence of the other species. The following description of the female of *C. zukeli* is based on that material:

DESCRIPTION.—Female body length 9.0 mm, macropterous, length of forewing 7.8 mm, subgenital plate with hind margin straight and recessed, muscle insertions lateral from posterior margin darkly colored, small, spurious sclerites absent from membrane between sterna 7 and 8.

MATERIAL.—Female, Idaho, Latah Co., Little Boulder Creek at Little Boulder Creek Campground, 26 April 1985, R. W. Baumann and C. R. Nelson; (BYU).

DISTRIBUTION.—IDAHO: Latah Co.: Potlatch River, Moscow Mt. 3,500–4,800 feet, Palouse River, Troy Creek, Spring Valley Creek near reservoir, Little Boulder Creek; (176). 1 April–12 May.

NOTES.—This unusual species lives in the same area as several other endemic capniids, *Capnura venosa* and *Capnia lineata*. This species resembles the latter of these two species but seems to be distinct from it in both sexes.

Species of Uncertain Taxonomic Status

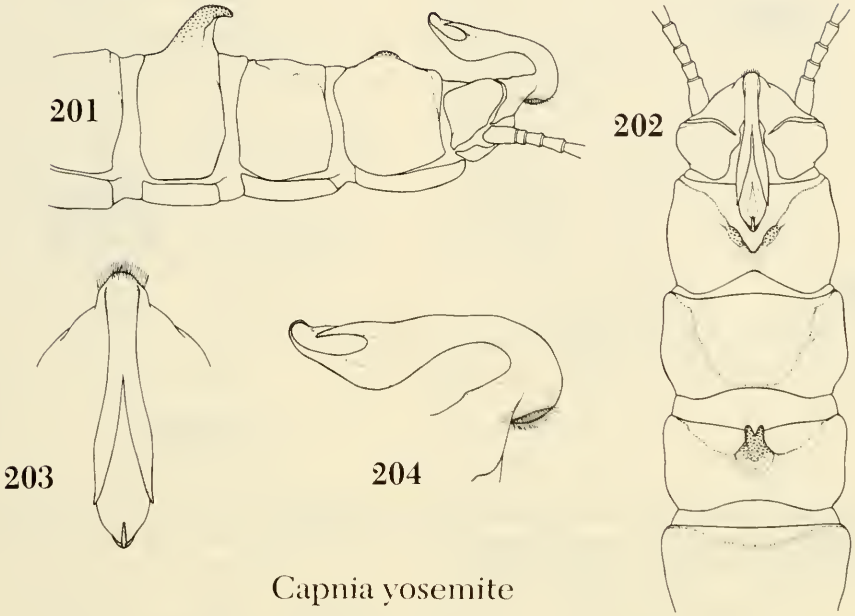
Capnia erecta Jewett

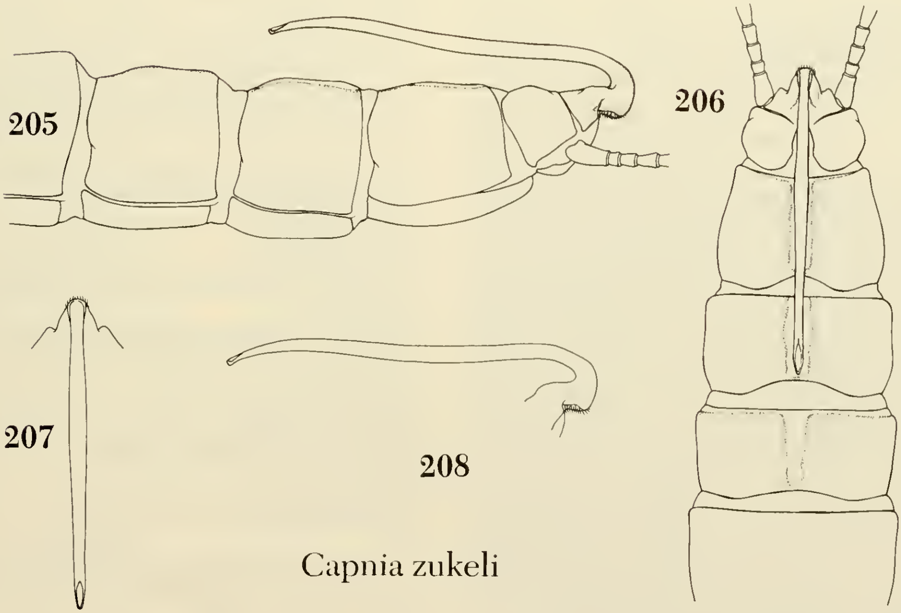
Map Fig. 272

Capnia erecta Jewett 1955: 147, 1959: 45. Illies 1966: 137. Stark et al. 1986: 385.

HOLOTYPE.—Male, Oregon; Josephine Co., Grave Creek, tributary of Rogue River, at Highway 99, 3 March 1950, S. G. Jewett, Jr.; (CAS).

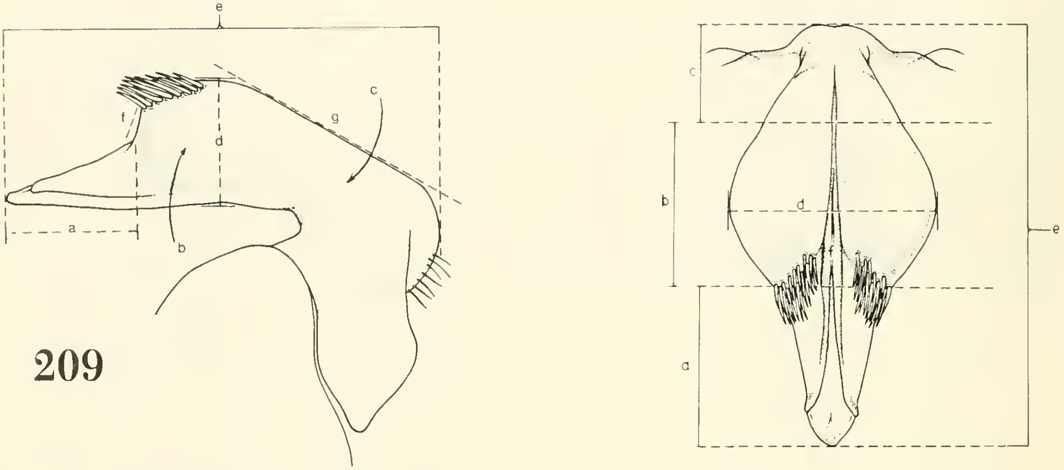
DIAGNOSIS.—This species is represented by a single male specimen that differs from all other members of the genus in having the epiproct not completely curved back over the abdomen. The specimen may be teneral so that the epiproct has not yet fully reflexed over the abdomen in the normal position of that of other *Capnia*. The shape of the epiproct most closely resembles that of *C. willametta*, with which it may be conspecific. The epiproct has a few rear-directed bristles on the upward-facing surface. Similar bristles are seen in several members of the Nana group, including *C. licina* and *C. glabra*. Further collecting of specimens from the type locality would be desirable to ascertain the correct placement of this strange specimen.





Figs. 201–204. *Capnia yosemite* Nelson & Baumann: 201, male terminalia, lateral; 202, male terminalia, dorsal; 203, male epiproct, dorsal; 204, male epiproct, lateral. California, Mariposa Co., Big Creek, Hwy 41, Summerdale Campground above Fish Camp, 18 March 1985, R. W. Baumann and C. R. Nelson.

Figs. 205–208. *Capnia zukeli* Hanson: 205, male terminalia, lateral; 206, male terminalia, dorsal; 207, male epiproct, dorsal; 208, male epiproct, lateral. Idaho, Latah Co., Little Boulder Creek, Little Boulder Creek Campground, 26 April 1985, R. W. Baumann and C. R. Nelson.



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Figs. 209–210. *Capnia decepta* (Banks): 209: male epiproct, lateral view; a, tip; b, bulb; c, neck; d, epiproct depth; e, epiproct length; f, anterior declivity; g, posterior declivity. 210: male epiproct, dorsal view; a, tip length; b, bulb length; c, neck length; d, epiproct width; e, epiproct length.

ACKNOWLEDGMENTS

We thank the many persons who provided specimens and lodging facilities during the course of this revision. The most gratifying part of this work was the hospitality and willingness to share both materials and ideas which we experienced while hunting and gathering these winter stoneflies. We particularly thank Jean A. Stanger for the fine line drawings. Gene and Lola Fiala took numerous trips throughout the Pacific Northwest seeking particular species of *Capnia* for which we required fresh specimens. We also thank Gene for testing some of the keys and reviewing the manuscript. Dr. Boris C. Kondratieff enthusiastically gave of his time to collect for and with us under difficult circumstances; he also aided us by reviewing the manuscript and testing the keys on his Aquatic Entomology students. We thank Dr. William D. Shepard and his Aquatic Entomology students for reading the manuscript and testing some of the keys. We give special thanks to our families who endured the long periods of time when we were away from family duties while gathering information and compiling the data for this work. Any errors remaining are our own.

We thank the curators and collections managers at the following institutions:

N. H. Anderson, Oregon State University,
Corvallis, Oregon.

P. H. Arnaud, Jr., California Academy of Sciences,
San Francisco, California.

M. A. Brusven, University of Idaho, Moscow, Idaho.

J. C. Burne, University of Wyoming, Laramie, Wyoming.

S. G. Cannings, University of British Columbia,
Vancouver, British Columbia, Canada.

J. A. Chemsak, University of California,
Berkeley, California.

W. H. Clark, Idaho Department of Health and Welfare,
Boise, Idaho.

T. D. Eichlin, California Department of Food and
Agriculture, Sacramento, California.

D. K. Faulkner, San Diego Museum of Natural History,
San Diego, California.

O. S. Flint, Jr., Smithsonian Institution,
Washington, D.C.

S. I. Frommer, University of California,
Riverside, California.

W. J. Hanson, Utah State University, Logan, Utah.

P. P. Harper, University of Montreal,
Montreal, Quebec, Canada.

C. A. Hogue, Natural History Museum of
Los Angeles County, Los Angeles, California.

D. H. Kavanaugh, California Academy of Sciences,
San Francisco, California.

B. C. Kondratieff, Colorado State University,
Fort Collins, Colorado.

R. J. Lavigne, University of Wyoming,
Laramie, Wyoming.

V. F. Lee, California Academy of Sciences, San Francisco, California.

J. E. H. Martin, Canadian National Collection, Ottawa, Ontario, Canada.

K. C. McGiffen, Illinois Natural History Survey, Champaign, Illinois.

T. E. Moore, University of Michigan, Ann Arbor, Michigan.

C. A. Olson, University of Arizona, Tucson, Arizona.

N. D. Penny, California Academy of Sciences, San Francisco, California.

W. E. Ricker, Nanaimo, British Columbia, Canada.

G. Roemhild, Montana State University, Bozeman, Montana.

R. T. Schuh, American Museum of Natural History, New York, New York.

R. O. Schuster, University of California, Davis, California.

S. Shaw, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

W. D. Shepard, California State University, Sacramento, California.

E. H. Smith, Chicago Field Museum, Chicago, Illinois.

S. D. Smith, Central Washington University, Ellensburg, Washington.

B. P. Stark, Mississippi College, Clinton, Mississippi.

K. W. Stewart, University of North Texas, Denton, Texas.

M. K. Thayer, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

G. W. Ulrich, University of California, Berkeley, California.

C. Vogt, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

D. W. Webb, Illinois Natural History Survey, Champaign, Illinois.

G. B. Wiggins, Royal Ontario Museum, Toronto, Ontario, Canada.

R. S. Zack, Washington State University, Pullman, Washington.

We thank the many people who have permitted us to share their homes with them, listened to our ideas and advised us, or given other special helps. We hope that seeing this revision is some compensation for the support they have given:

F. L. Andersen, Brigham Young University, Provo, Utah.

E. Brown, Prescott, Arizona.

D. Callahan, Bishop, California.

D. & T. Collazo, Ramsey Canyon Preserve, Hereford, Arizona.

G. R. & L. Fiala, Gresham, Oregon.

G. & L. Larsen, Clovis, California.

G. & M. Longhurst, Nuevo Casas Grandes, Chihuahua, Mexico.

J. K. Nelson, Provo, Utah.

J. R., A. J., & A. L. Nelson, Provo, Utah.

W. P. & A. L. Nelson, Brigham City, Utah.

W. R., J. O., N. R., & C. R. Nelson, Anaheim Hills, California.

A. & E. Pratt, Nuevo Casas Grandes, Chihuahua, Mexico.

J. A. Stanger, Willows, California.

P. & K. Wheeler, Logandale, Nevada.

R. White, Ontario, Oregon.

A. R. Whitehead, Brigham Young University, Provo, Utah.

V. & H. Young, Ely, Nevada.

Without the combined help of these persons and members of the Winter Stonefly Club this research would not have been possible:

A. Allen, Boise, Idaho.

R. D. Anderson, Southern Utah State College, Cedar City, Utah.

C. W. Baker, Boise State University, Boise, Idaho.

J. R. Barnes, Brigham Young University, Provo, Utah.

A. H. Barnum, Dixie College, St. George, Utah.

G. T. Baxter, University of Wyoming, Laramie, Wyoming.

R. C. Biggam, University of Idaho, Moscow, Idaho.

R. L. Bottorff, University of California, Davis, California.

D. J. Burdick, California State University, Fresno, California.

D. K. Burton, University of Manitoba, Winnipeg, Manitoba, Canada.

S. J. Cary, New Mexico Environmental Improvement Division, Santa Fe, New Mexico.

S. M. Clark, Brigham Young University, Provo, Utah.

K. Clement, California State University, Chico, California.

M. D. Coffey, Southern Oregon State College, Ashland, Oregon.

E. M. Coombs, Treasure Valley Community College, Ontario, Oregon.

S. D. Cooper, University of California, Santa Barbara, California.

A. J. Cordone, California Department of Fish and Game, Sacramento, California.

C. E. Cushing, Battelle Laboratories, Richland, Washington.

R. D. Cutter, Tahoe City, California.

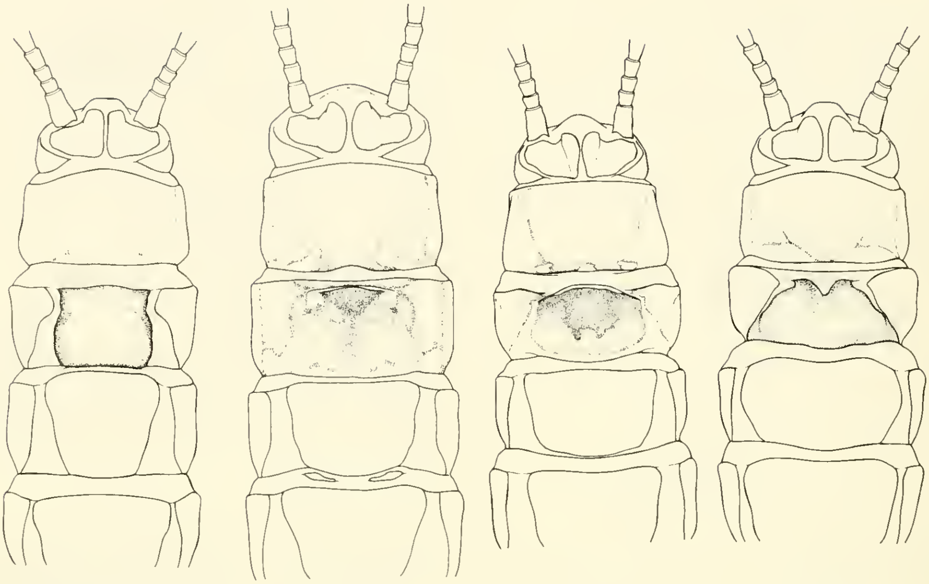
J. M. Deinstadt, California Fish and Game, Rancho Cordova, California.

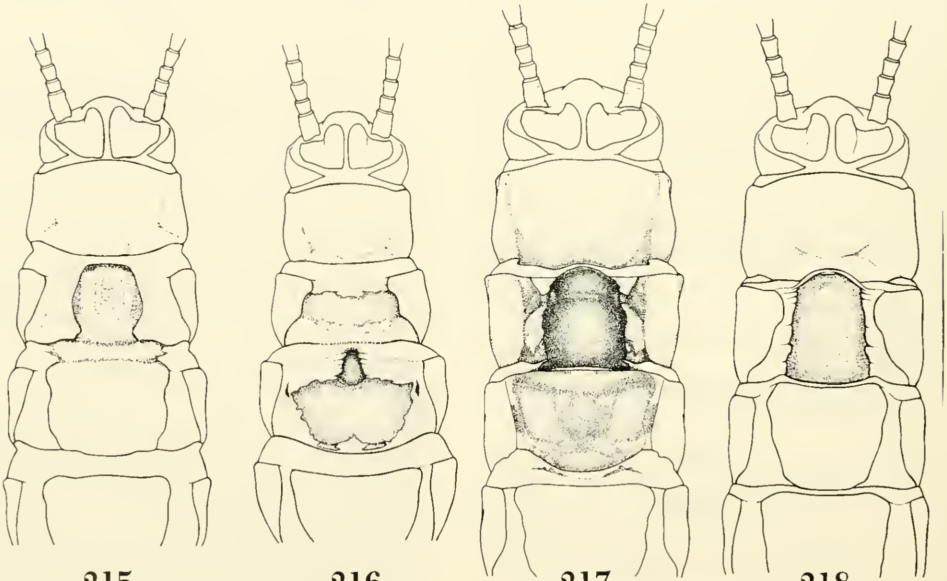
D. G. Denning, Moraga, California.

R. L. Denton, Utah Department of Health, Salt Lake City, Utah.

K. A. Dobry, Canoga Park, California.

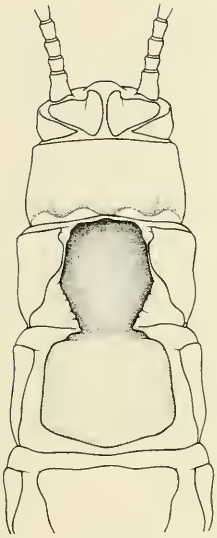
D. B. Donald, Canadian Wildlife Service, Edmonton, Alberta.





Figs. 211–214. *Capnia* spp.: 211, *C. barberi*, California, Plumas Co., Long Valley Creek, Hwy 70, Cromberg, 14 February 1985, R. W. Baumann and C. R. Nelson.; 212, *C. californica*, California, Shasta Co., South Fork Clear Creek above Igo, 16 February 1985, R. W. Baumann and C. R. Nelson; 213, *C. californica*, Arizona, Gila Co., Strawberry Creek, Hwy 87, Strawberry, 14 January 1984, R. W. Baumann and C. R. Nelson; 214, *C. cheama*, Montana, Lincoln Co., Kootenai River, 19 March 1970, R. L. Newell.

Figs. 215–218. *Capnia* spp.: 215, *C. coloradenis*, Routt Co., Colorado, Willow Creek near Hahns Peak, 13 May 1968, B. R. Oblad.; 216, *C. confusa*, Montana, Lincoln Co., Kootenai River, 28 March 1970, R. L. Newell; 217, *C. coyote*, California, San Bernardino Co., Seeley Creek, Hwy 138, Camp Seeley, 5,000 feet, 9 January 1988, R. W. Baumann, B. C. Kondratieff, C. R. Nelson, B. Sargent; 218, *C. decepta*, Arizona, Coconino Co., West Fork Oak Creek, near confluence with Oak Creek, 13 January 1984, R. W. Baumann and C. R. Nelson.



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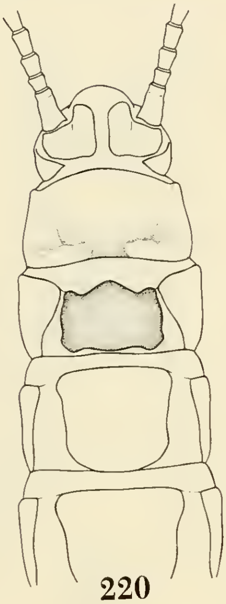

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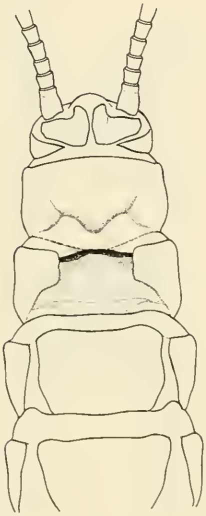

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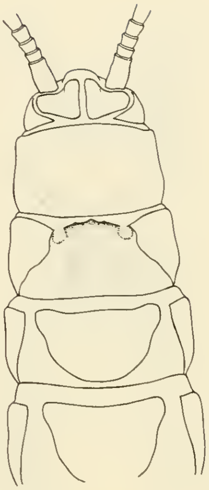

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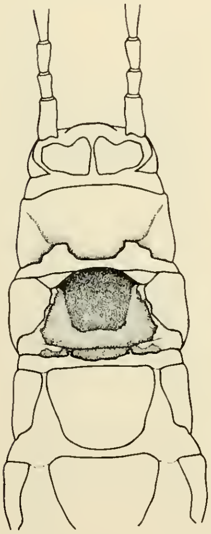

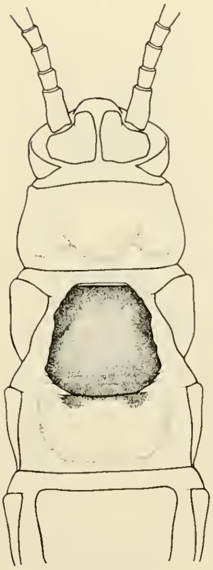

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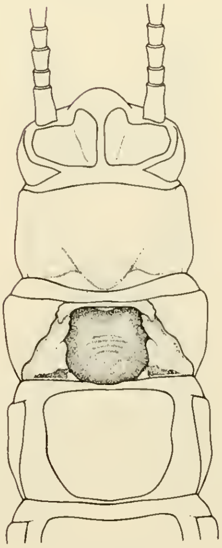

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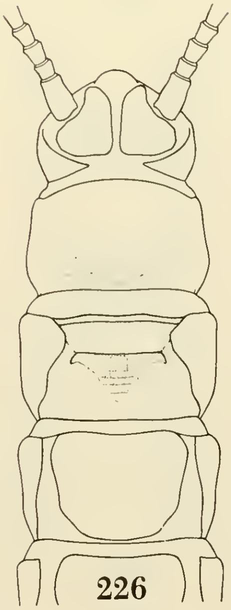

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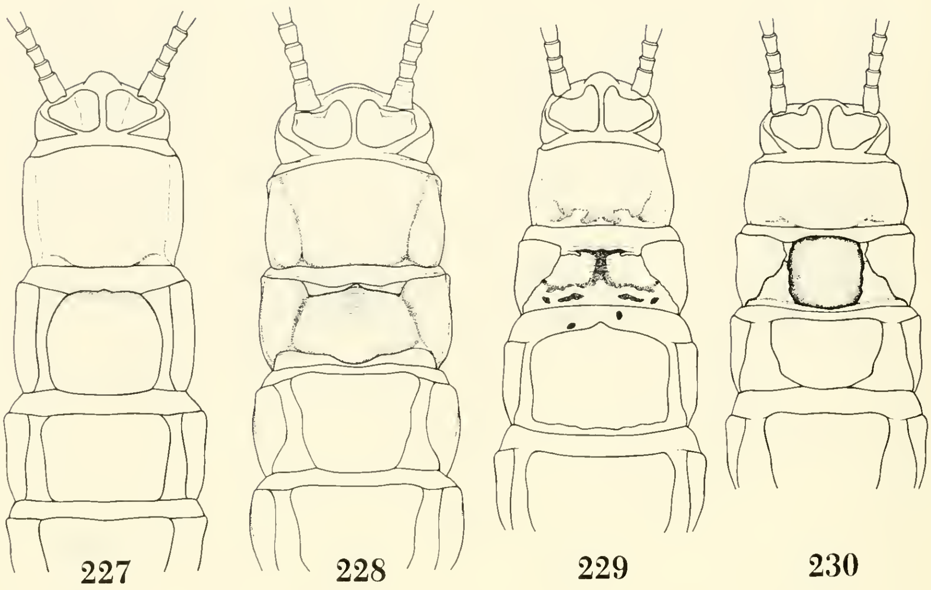
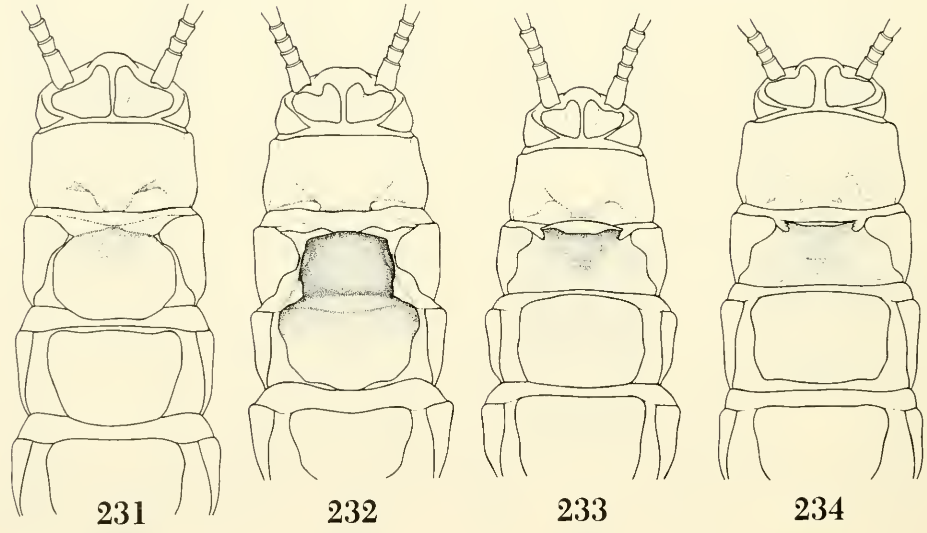
Figs. 219–222. *Capnia* spp.: 219, *C. elongata*, California, Placer Co., North Fork American River near Colfax, 21 February 1985, R. W. Baumann and C. R. Nelson; 220, *C. excavata*, California, Plumas Co., Mosquito Creek at junction North Fork Feather River, 14 February 1985, R. W. Baumann and C. R. Nelson.; 221, *C. glabra*, California, Placer Co., Ward Creek, Hwy 89, near Lake Tahoe, 22 February 1985, R. W. Baumann and C. R. Nelson; 222, *C. gracilaria*, Montana, Missoula Co., Rattlesnake Creek above Greenough Park, Missoula, 17 March 1969, R. W. Baumann.

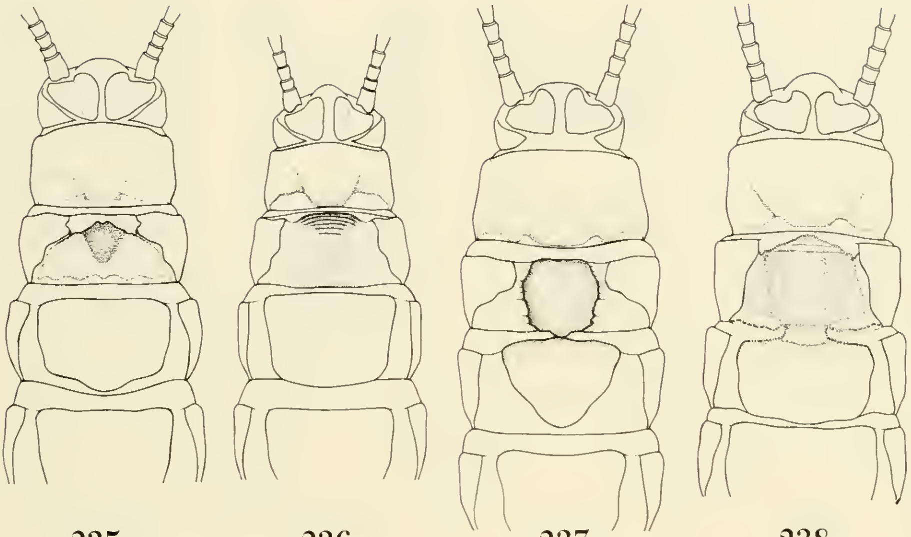
Figs. 223–226. *Capnia* spp.: 223, *Capnia hitchcocki*, California, Alameda/Santa Clara County line, Arroyo Mocho Creek, 20 miles south Livermore, San Antonio Valley Road, 19 March 1985, R. W. Baumann and C. R. Nelson; 224, *C. hornigi*, Nevada, Esmeralda Co., White Mountains, Middle Creek, 10 February 1977, A. L. Sheldon; 225, *C. inyo*, California, Inyo Co., Independence Creek, Grays Meadow Campground, 25 January 1985, R. W. Baumann and C. R. Nelson; 226, *C. jewetti*, Oregon, Clatsop Co., Clatskanine River, Olney, 15 February 1946, S. G. Jewett, Jr.





Figs. 227–230. *Capnia* spp.: 227, *C. lacustra*, California, El Dorado Co., Lake Tahoe, Emerald Bay, depth 116–198 feet, 11 July 1962, T. C. Frantz and A. J. Cordone; 228, *C. licina*, Oregon, Clackamas Co., Upper Salmon River, near junction Hwy 26 and State Road 35, 28 April 1984, G. R. Fiala; 229, *C. lineata*, Idaho, Latah Co., Little Boulder Creek, Little Boulder Creek Campground, 26 April 1985, R. W. Baumann and C. R. Nelson; 230, *C. mariposa*, California, Mariposa Co., Tuolumne River, Hwy 120, Tuolumne Meadows Campground, 27 June 1988, R. W. Baumann and J. A. Stanger.

Figs. 231–234. *Capnia* spp.: 231, *C. melia*, Oregon, Clackamas Co., Wildcat Creek, Hwy 36, 1 mile east of Alder Creek, 2 March 1984, R. W. Baumann, C. R. Nelson, and G. R. Fiala; 232, *C. mono*, California, Mono Co., Slinkard Creek, 2 miles north of Topaz, 5 November 1983, W. D. Shepard, reared from nymph in laboratory; 233, *C. nana nana*, British Columbia, Terrace, 1936, M. E. Hippisley; 234, *C. nana wasatchae*, Utah, Cache Co., Logan Canyon, Springhollow, tributary of Logan River, 4 January 1984, C. R. Nelson and S. A. Wells.



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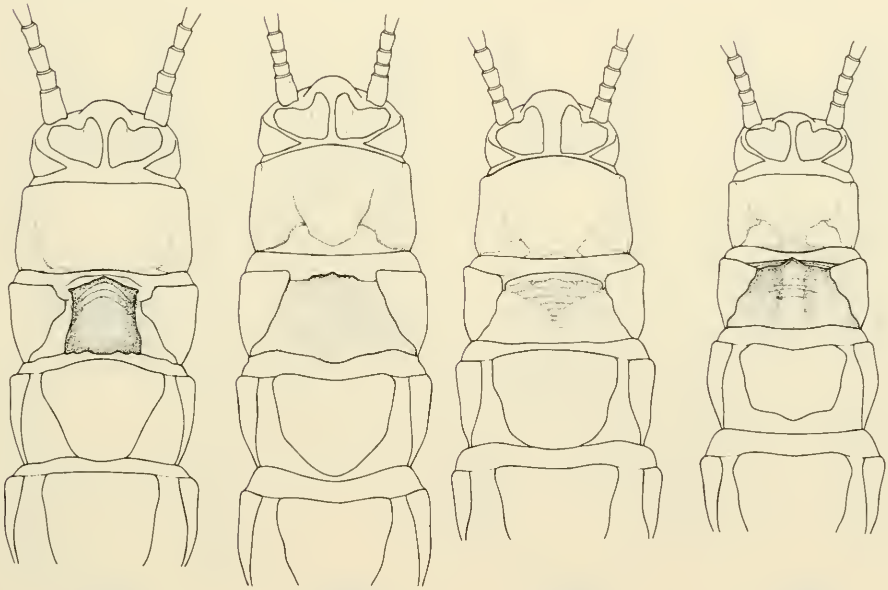

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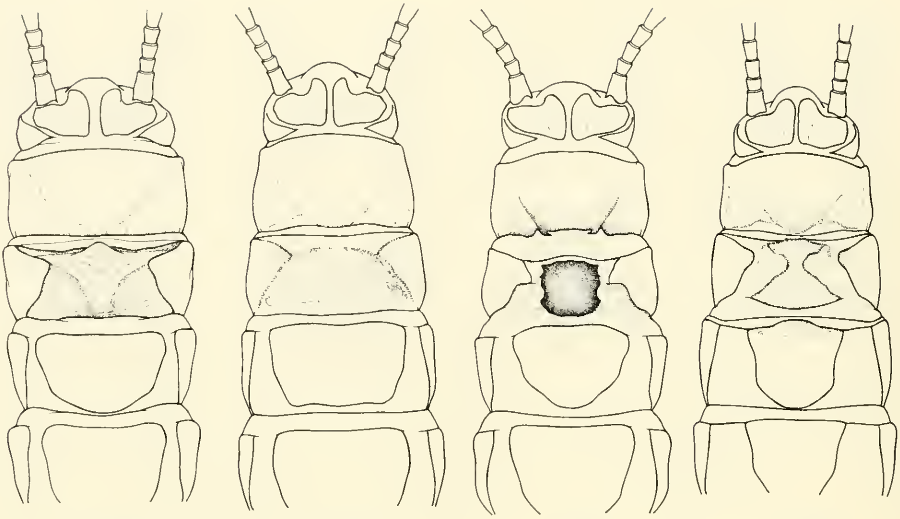
Figs. 235–238. *Capnia* spp.: 235, *C. nearctica*, Northwest Territories, Keewatin District, Baffin Island, Nettilling Lake, 6 July 1956; 236, *C. oregona*, Oregon, Linn Co., Gordon Meadows, 4,000 feet, 18 July 1959, H. Hacker; 237, *C. palomar*, California, San Diego Co., Palomar Mountain, Fry Creek, Road S–6, Fry Creek Campground, 18 January 1985, R. W. Baumann and C. R. Nelson; 238, *C. petila*, Utah, Box Elder Co., Raft River Mountains, Fisher Creek at mouth of canyon, 29 March 1979, R. W. Baumann and G. M. Webb.

Figs. 239–242. *Capnia* spp.: 239, *C. pileata*, Oregon, Clackamas Co., 0.6 miles north of Marquam, 15 January 1967, S. G. Jewett, Jr.; 240, *C. promota*, Oregon, Benton Co., Corvallis, Oak Creek, 1 January 1936.; 241, *C. quadrituberosa*, California, Butte Co., small stream north of Oroville near Garden Drive, 15 February 1985, R. W. Baumann and C. R. Nelson; 242, *C. regilla*, California, Marin Co., Bear Valley Creek, Point Reyes National Seashore, 25 May 1975, D. G. Denning.



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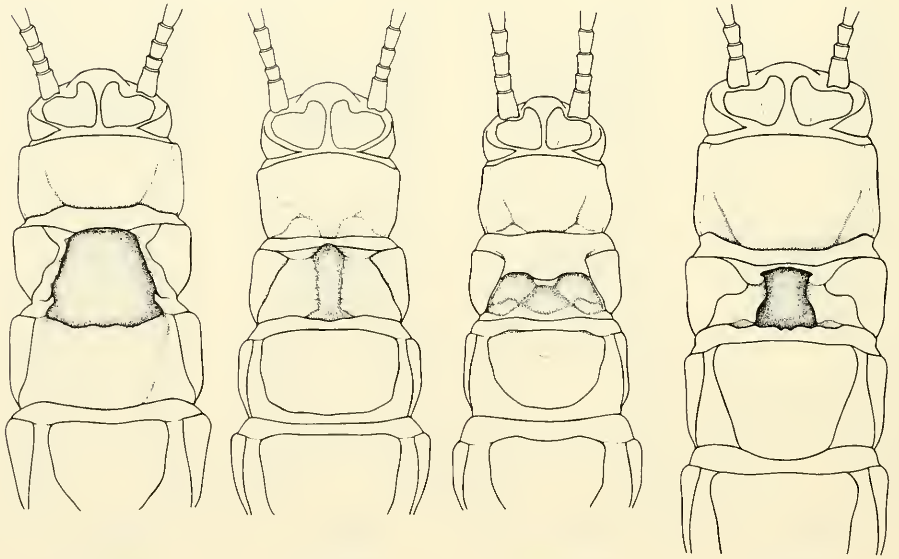

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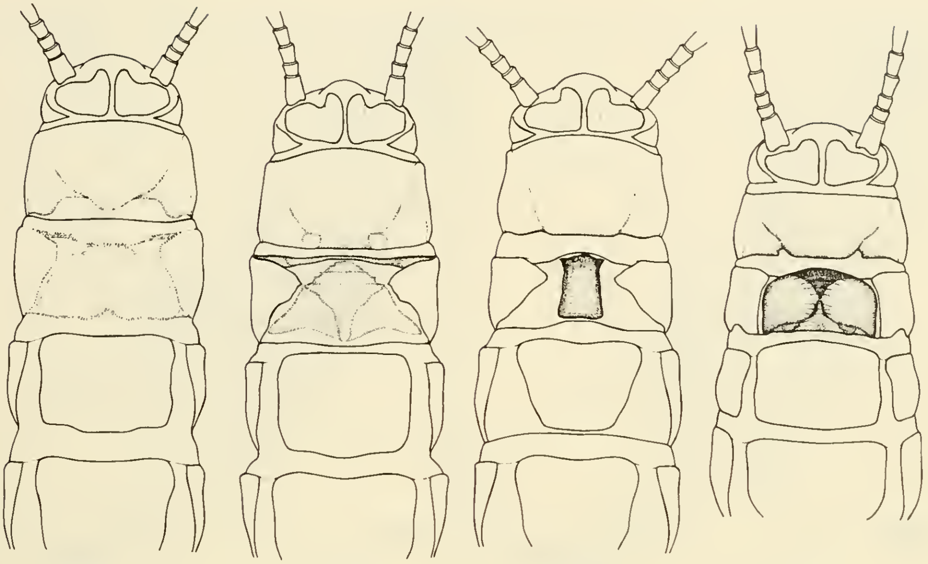
Figs. 243–246. *Capnia* spp.: 243, *C. saratoga*, California, near Saratoga, 25 February 1940, S. G. Jewett, Jr.; 244, *C. scobina*, California, Nevada Co., Sagehen Creek, 6,300 feet, 15 February 1965, A. L. Sheldon; 245, *C. sequoia*, California, Tuolumne Co., Ackerson Creek, Evergreen Lodge Road, 18 March 1985, R. W. Baumann and C. R. Nelson; 246, *C. sextuberculata*, Oregon, Wallowa Co., Lake Creek, junction Lostine River, Lostine Guard Station, 19 May 1977, R. W. Baumann and D. Dunster.

Figs. 247–250. *Capnia* spp.: 247, *C. shepardi*, California, Mono Co., Lee Vining Creek, Lee Vining Campground, 14 March 1985, R. W. Baumann and C. R. Nelson; 248, *C. spinulosa*, California, Los Angeles Co., San Gabriel Mountains, 0.5 miles northeast of Camp Valcrest, 24 April 1977, C. L. Hogue.; 249, *C. teresa*, California, San Bernardino Co., San Antonio Creek, at Mount Baldy Village, 22 January 1985, R. W. Baumann and C. R. Nelson; 250, *C. tumida*, California, Plumas Co., Big Grizzly Creek, junction tributary of Middle Fork Feather River, Hwy 70, 14 February 1985, R. W. Baumann and C. R. Nelson.



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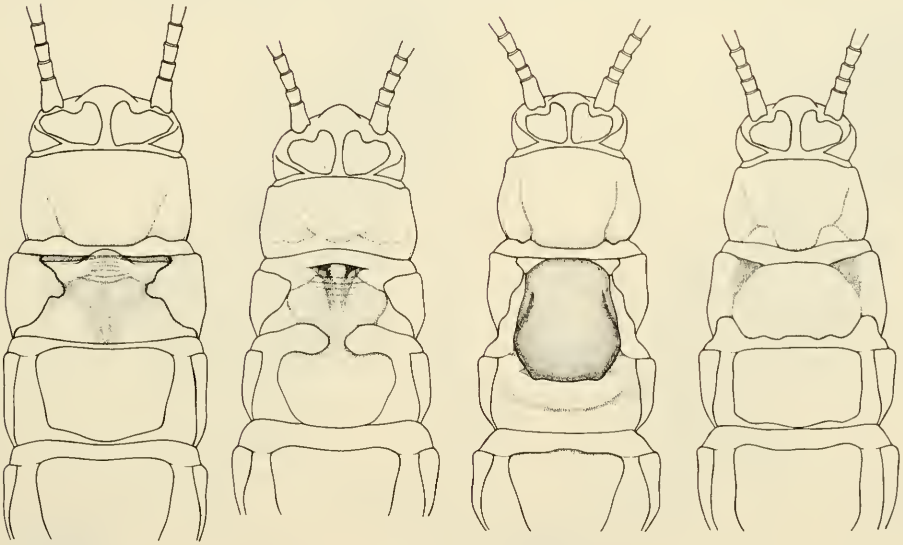

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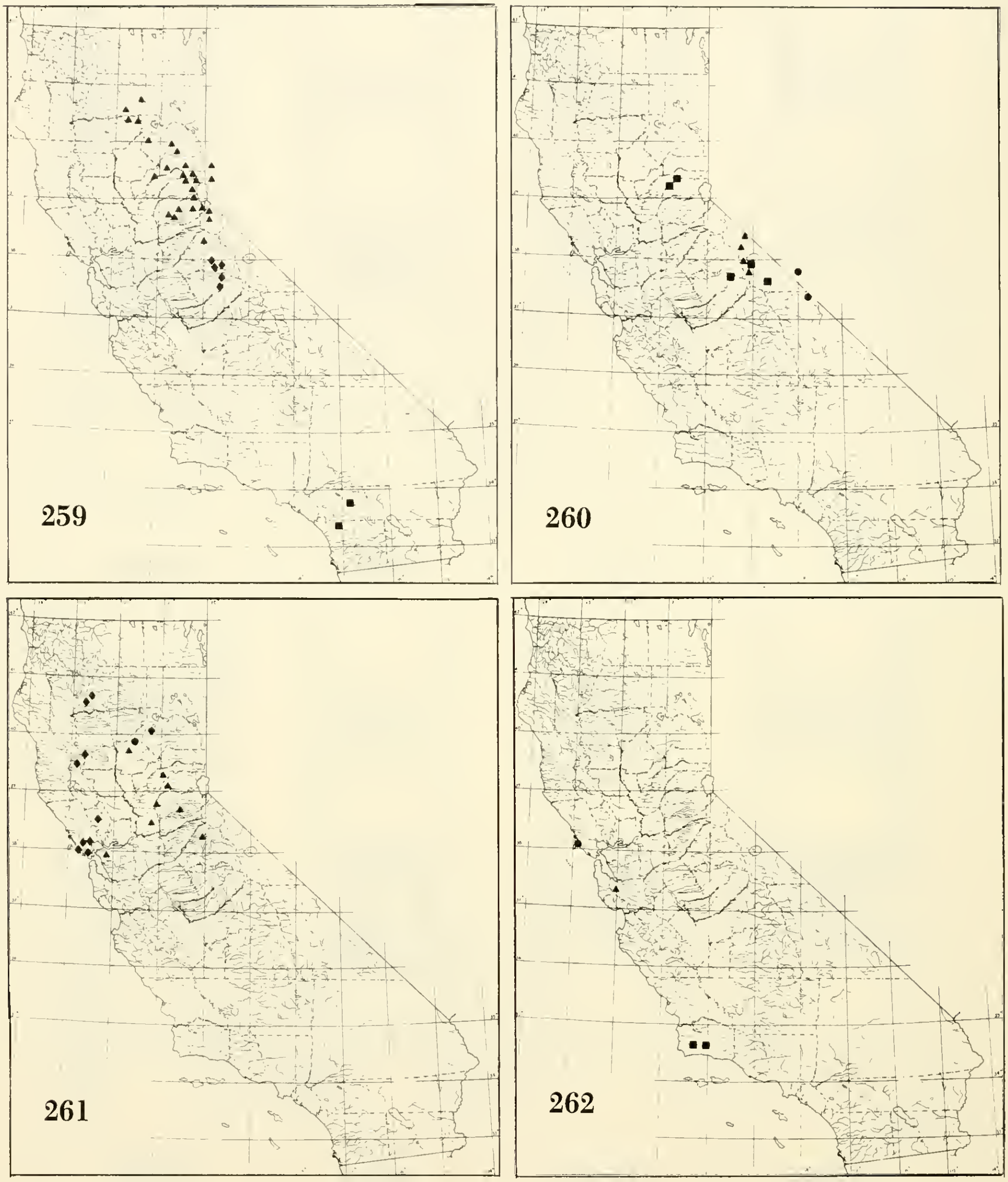
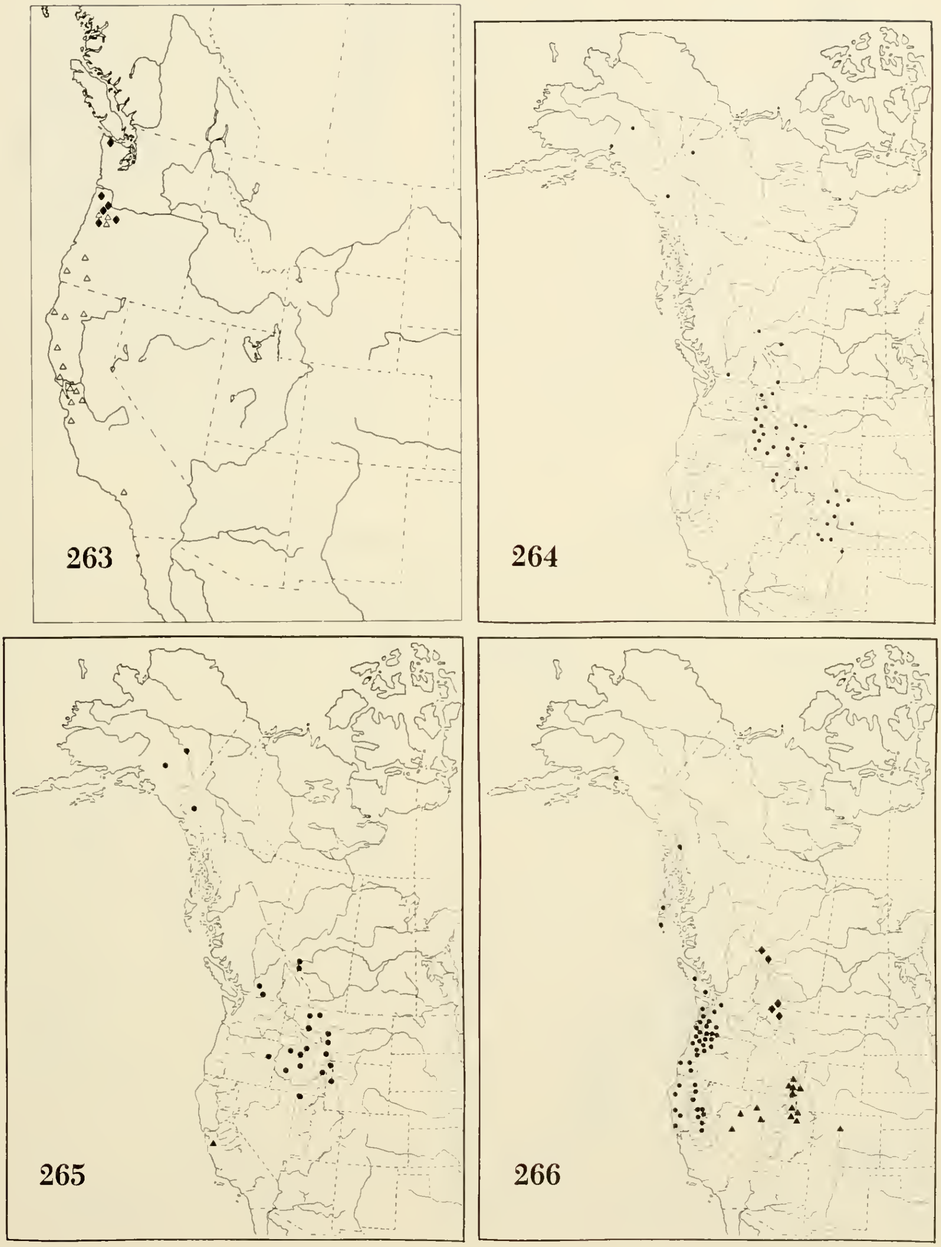
Figs. 251–254. *Capnia* spp.: 251, *C. uintahi*, Utah, Wasatch Co., Provo River, Stewarts Ranch, 2 March 1949, A. R. Gaufin; 252, *C. umpqua*, California, Shasta Co., Sulphur Creek, Castle Crags State Park, 16 February 1985, R. W. Baumann and C. R. Nelson.; 253, *C. utahensis*, Utah, Beaver Co., South Creek, 0.5 miles south of Beaver, 21 February 1965, A. V. Nebeker; 254, *C. valhalla*, California, Los Angeles Co., San Gabriel Mountains, 0.5 miles east of Horseflat Road, 6 March 1977, C. L. Hogue, no. 229.

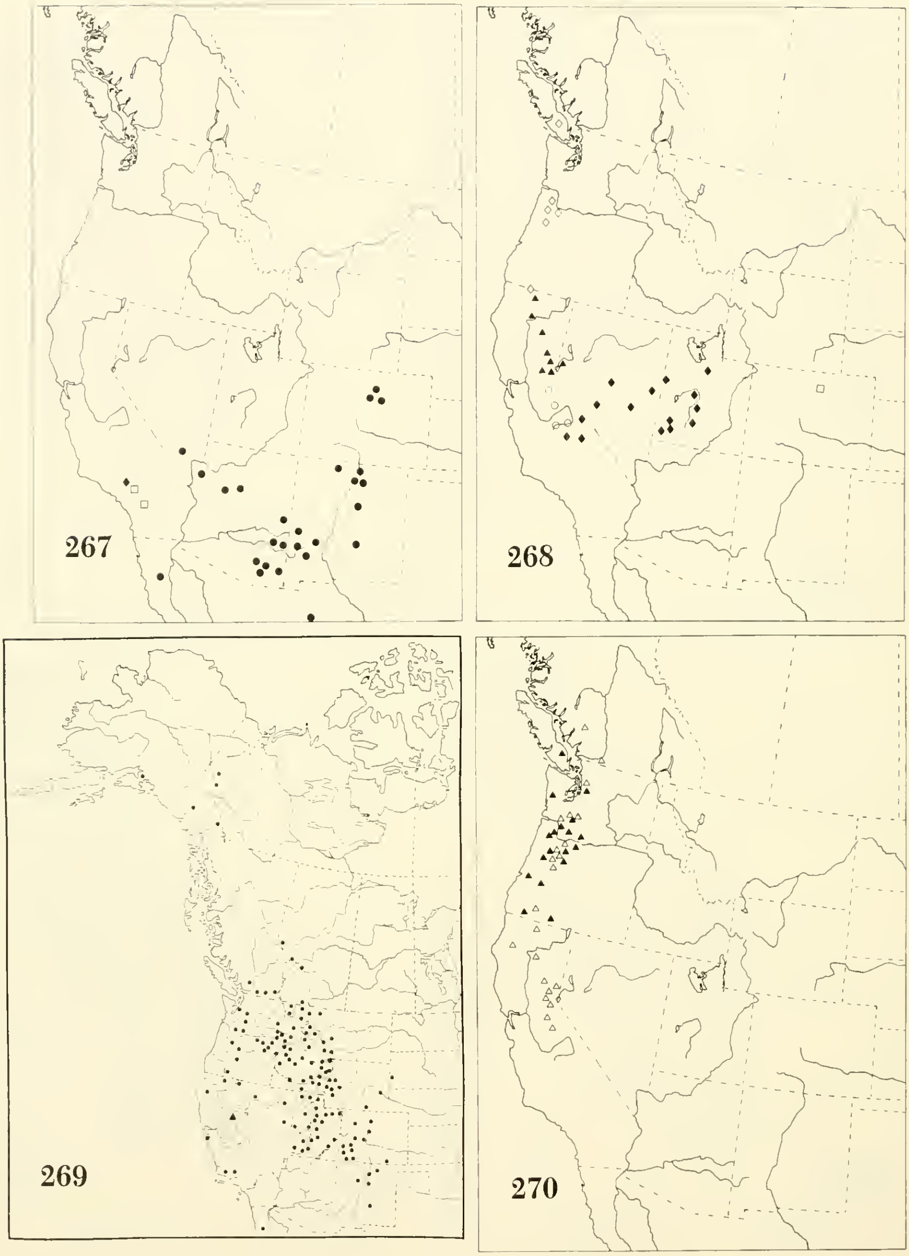
Figs. 255–258. *Capnia* spp.: 255, *C. ventura*, California, Ventura Co., Bear Creek, Wheeler Gorge Campground north of Ojai, 23 January 1985, R. W. Baumann and C. R. Nelson; 256, *C. vernalis*, Montana, Broadwater Co., Missouri River, Toston, 28 March 1952, R. Hays; 257, *C. yosemite*, California, Mariposa Co., Big Creek, Hwy 41, Summerdale Campground above Fish Camp, 18 March 1985, R. W. Baumann and C. R. Nelson; 258, *C. zukeli*, Idaho, Latah Co., Little Boulder Creek, Little Boulder Creek Campground, 26 April 1985, R. W. Baumann and C. R. Nelson.



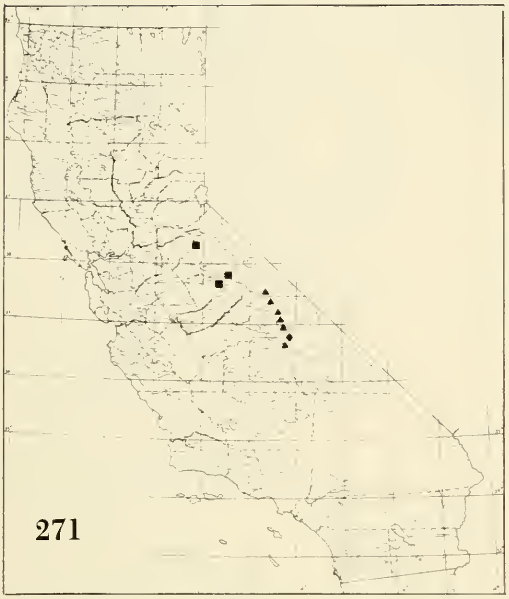
Figs. 259–262. Distributional maps *Capnia* spp.: 259, *C. barberi* solid triangles, *C. palomar* solid squares, and *C. yosemite* solid diamonds; 260, *C. hornigi* solid circles, *C. mono* solid triangles, and *C. shepardi* solid squares; 261, *C. californica* solid diamonds (California distribution, see Fig. 273 for complete distribution), *C. ophiona* solid circle, *C. quadrituberosa* solid triangles; 262, *C. regilla* solid circle, *C. saratoga* solid triangle, and *C. ventura* solid squares.

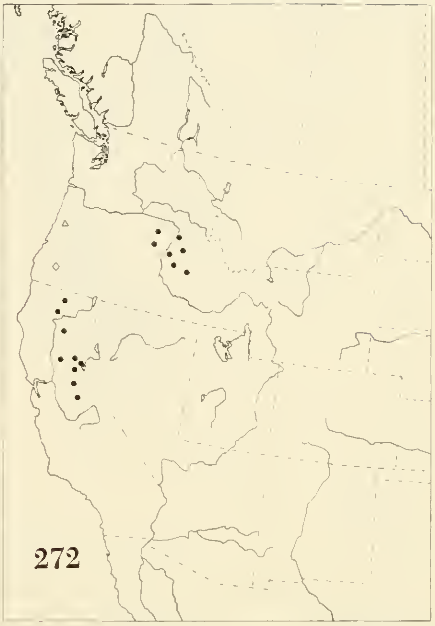


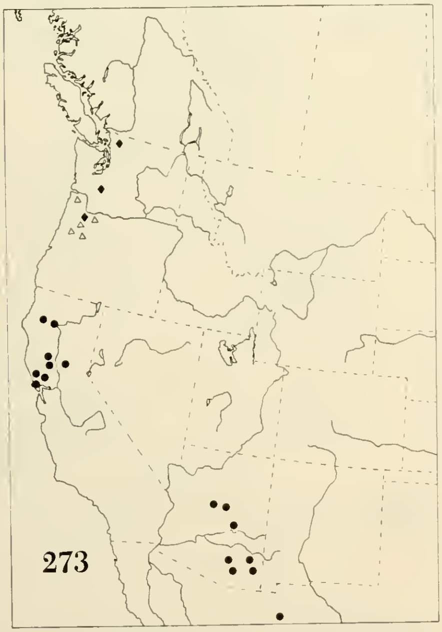
Figs. 263–266. Distributional maps *Capnia* spp.: 263, *C. jewetti* solid diamonds and *C. umpqua* open triangles; 264, *C. coloradensis* solid circles; 265, *C. hitchcocki* solid triangle, and *C. petila* solid circles; 266, *C. cheama* solid diamonds, *C. excavata* solid circles, and *C. uintahi* solid triangles.

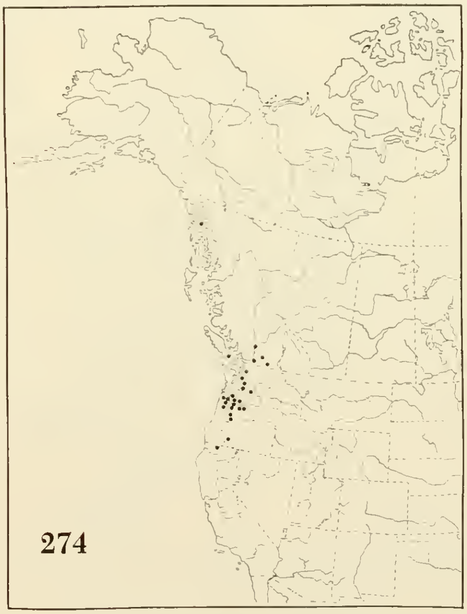


Figs. 267–270. Distributional maps *Capnia* spp.: 267, *C. coyote* solid diamond, *C. decepta* solid circles, and *C. teresa* open squares; 268, *C. arapahoe* open square, *C. pileata* open diamonds, *C. sequoia* open circles, *C. tumida* solid triangles, and *C. utahensis* solid diamonds; 269, *C. gracilaria* solid circles and *C. lacustra* solid triangle; 270, *C. elongata* open triangles and *C. promota* solid triangles.

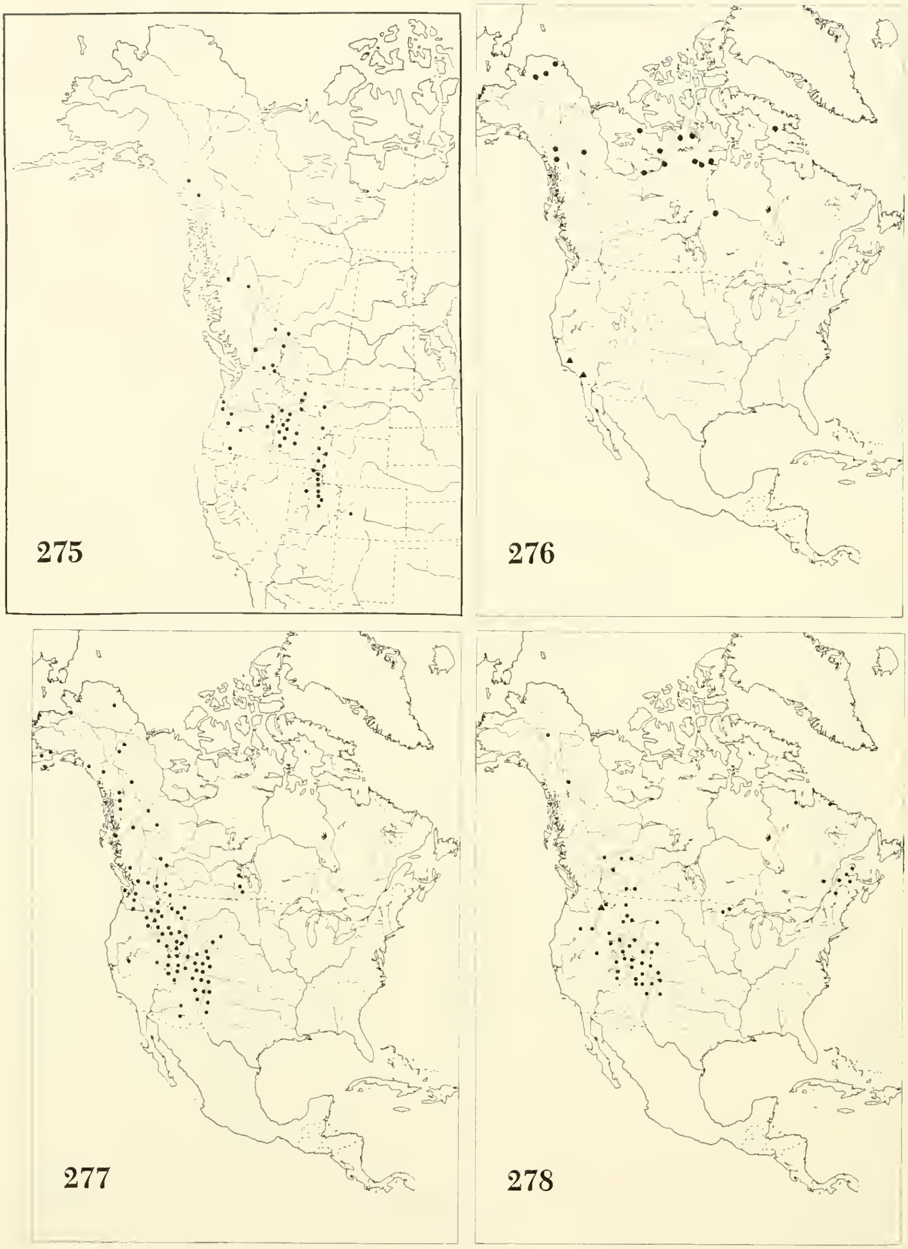




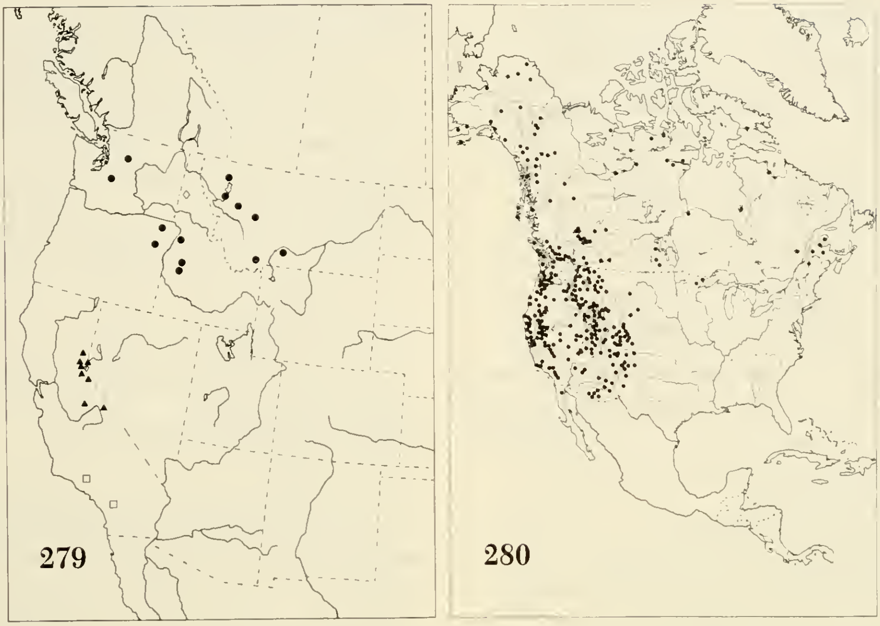




Figs. 271–274. Distributional maps *Capnia* spp.: 271, *C. giulianii* solid diamond, *C. inyo* solid triangles, and *C. mariposa* solid squares; 272, *C. erecta* open diamond, *C. glabra* solid circles, and *C. willametta* open triangle; 273, *C. californica* solid circles (total distribution, see Fig. 261 for detailed California distribution), *C. licina* solid diamonds, and *C. oregona* open triangles; 274, *C. melia* solid circles.



Figs. 275–278. Distributional maps *Capnia* spp.: 275, *C. nana* solid circles; 276, *C. nearctica* solid circles and *C. valhalla* solid triangles; 277, *C. confusa* solid circles; 278, *C. lineata* solid triangle and *C. vernalis* solid circles.



Figs. 279–280. Distributional maps *Capnia* spp.: 279, *C. scobina* solid triangles, *C. sextuberculata* solid circles, *C. spinulosa* open squares, and *C. zukeli* open diamond; 280, total recorded distribution of the genus *Capnia* in the Nearctic region solid circles.

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This project was funded by the M. L. Bean Life Science Museum, Department of Zoology, and College of Biological and Agricultural Sciences at Brigham Young University. Additional support for the senior author was provided by the Tilton Postdoctoral Fellowship Fund at the California Academy of Sciences. This financial support is gratefully acknowledged.

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MASS MORTALITY OF SALAMANDERS (*AMBYSTOMA TIGRINUM*) BY BACTERIA (*ACINETOBACTER*) IN AN OLIGOTROPHIC SEEPAGE MOUNTAIN LAKE

Kathleen Muriel Worthylake[1] and Peter Hovingh[2]

ABSTRACT.—Of the 13 lakes in the central Wasatch Mountains with tiger salamander (*Ambystoma tigrinum*) populations, salamander mass mortalities occurred in four seepage lakes that experienced extensive lowering of the water levels during the summer. The largest of these lakes, the oligotrophic Desolation Lake, was studied to determine the cause of the mortality phenomenon. The recurrent annual mass mortality involved both breeding adults and young-of-the-year. Rate kinetics suggest that mortality rate doubles with a fivefold increase in the number of aquatic young salamanders. The proximate cause of the mass mortality was identified as a bacterium, *Acinetobacter* sp. Desolation Lake and a seepage lake that did not experience the mass mortality were studied for the presence of *Acinetobacter*. Both lakes experienced two bacteria cycles: the first in early summer involved gram-positive bacteria, and the second in late summer involved gram-negative bacteria (mostly coliform bacteria and *Acinetobacter*). The mass mortalities were associated with the late-summer gram-negative bacterial bloom, and *Acinetobacter* was found in large numbers in Desolation Lake. Algae, as well as other photosynthetic plants, were not present in large numbers. Since these lakes are growth-limited with respect to nitrogen and not with respect to phosphate, and since Desolation Lake had extensive lowering of the lake level during the summer, the biological cycle of the lake is proposed to be due to atmospheric and sheep-produced nitrogen products within the watershed. In this unstable lake system, bacteria are primarily responsible for incorporation of nitrogen in the food chain. The timing of the cyclical events depends on total winter precipitation.

The biology of the tiger salamander (*Ambystoma tigrinum*) has been extensively described (Anderson et al. 1971, Collins 1981, Hassinger et al. 1970, Rose and Armentrout 1976, Semlitsch 1983, Sexton and Bizer 1978, and Tanner et al. 1971), but only one population has been described with pathological symptoms (Rose and Harshbarger 1977). This may not be unexpected in view of the fact that natural amphibian populations may not be prone to mass pathological events as shown by the scarcity of literature reports (Reichenbach-Klinke and Elkan 1965). Recently, a report of mass mortality of larval *Rana sylvatica* was attributed to the bacterium *Aeromonas* (Nyman 1986).

This paper describes the recurrent mass mortality of the tiger salamander in an oligotrophic seepage lake in the Wasatch Mountains, Utah. We found that the proximate cause of the deaths was due to the bacterium *Acinetobacter*. Because the mass mortality was recurrent, we were able to study the kinetics of the die-off as well as the presence of *Acinetobacter* in the lake. Furthermore, we suggest that the die-off of the tiger salamander in the seepage lake is in part attributed to the extensive lowering of the lake levels as well as the concentration of nitrogen in the snow and from the watershed. The combined information describes some of the biological features of seepage lakes in the Wasatch Mountains.

METHODS

Water sampling in the hypolimnion utilized the Kemmerer water sampling bottle. Water samples from the surface waters were taken from two points in the lake and combined. The samples were collected in the afternoon, placed on ice in the dark two hours after the collection time, and delivered the subsequent morning for bacterial, algal, or chemical analysis. Snow sampling occurred in early April from three points around Desolation Lake. The samples were analyzed for nitrites and nitrates (test kits from Aquarium Pharmaceuticals, Inc., Perkasie, Pennsylvania) and sulfates (Terho and Hartiala 1971) after the addition of 10 mg sodium carbonate (to prevent volatilization of the nitrites and nitrates), and concentrated to about 25 ml. Climatic data came from U.S. Climatological Data (1980–1986) taken at Silver Lake, Brighton (lat. 40° 36′ North, long. 111° 35′ West), at 2,666 m elevation in Big Cottonwood Canyon, Wasatch Mountains.

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The monitoring of dead adult salamanders involved the inspection of the lake, the shoreline, and the area beneath logs on the shoreline. The numbers of dead adults are thus minimal figures since some adults may have died undetected in the lake and under logs in the adjacent forest. The aquatic larval salamanders were counted as they were stranded on the shore and in the adjacent waters. Most of the salamanders could be counted in this manner, and very few were observed in the lake bottoms. The exception to this occurred in 1986 when many of the aquatic young salamanders sank to the bottom and could not be inventoried. The inventory involved the relocation of all dead salamanders such that they would not be counted twice.

Histological analysis was performed by Dr. J. Harshbarger at the Registry of Tumors in Lower Animals, Smithsonian Institution, Washington, D.C. Algal analysis involved both the determination of chlorophyll *a* (corrected for the presence of degradation products) by M. A. Nielsen, Ecosystem Research Institute, Logan, Utah, and algal counts and identification by Dr. R. I. Lynn, Department of Biology, Utah State University, Logan, Utah. Chemical analysis was performed by Utah State University Water Research Laboratory, Logan, Utah.

Bacteria were enumerated as viable counts by the plate count technique using 5% sheep blood in tryptic soy agar. Identification of bacteria was by standard biochemical methods (Lennette et al. 1985). The plate count method was selected as we were examining the cause of the salamander deaths. We then extended the observations to the lake with the same plate count technique to determine the presence of these bacteria in the lake. Although viable counts have limitations as to "seeing" fast-growing colonies at the expense of slow-growing colonies, two circumstances justify the use of viable counts in this research: (1) specific groups (gram-negative versus gram-positive and the determination of the pathogens *Acinetobacter*, *Pseudomonas*, and coliform bacteria) were counted, and (2) a perturbation in the lake (mass mortality of the salamanders) was being monitored. Thus, two of the three acceptable circumstances for using viable count methodology were met (Fry 1982).

To demonstrate that *Acinetobacter* was the cause of the salamander mortality, we placed two salamanders (obtained from lakes that did not experience the mass mortality) in 8 liters of water. The water was inoculated with approximately 300 million colony-forming, live bacteria obtained from diseased salamanders or from Desolation Lake in the case of *Escherichia coli*. After the disease developed, the bacteria were identified from the salamander. Koch's postulates for the cause of a disease from terrestrial animals require that bacteria be taken from a lesion of the diseased animal and that after inoculation of a healthy animal this same bacteria be isolated from the new lesions. Aquatic animals present a variation on this procedure since the lesion is in water and water may contain other pathogens and bacteria. Thus, the bacteria were isolated from the peritoneum of the salamander and inoculated in the water that contained the salamanders.

DESCRIPTION OF THE LAKES AND SALAMANDER BIOLOGY IN THE CENTRAL WASATCH MOUNTAINS

Desolation Lake is the largest of the seepage lakes under study in the Wasatch Mountains. Desolation Lake has no surface inflows and outflows (definition of seepage lake, Pennak 1968), receives all its water from snowmelt, has extensive shorelines of soil, and has a paucity of contiguous rock abutments. It occurs in Big Cottonwood drainage at 2,820 m elevation and covers approximately 0.042-km^2 surface area in a 0.7-km^2 glaciated bowl.

During the atypically wet years of 1983 and 1984 the 10-m-deep lake dropped 4 m during the summer (Fig. 1). During a more average year (1985) it dropped 2 m while starting at a lower level in July. The lake dropped at a rate of 5 cm per day in July of the wet years until it reached the more typical level, at which time the lake continued to drop 2 cm per day for the remainder of summer. In early summer thermostratification occurs at the 6-m-deep level; this thermostratification disappears as the lake level drops. For two months the surface temperature of the lake is above 15 C (Fig. 1).

The total dissolved solids (46 mg/ml) consisted mostly of calcium bicarbonate (40.3 mg/l) in the surface waters in 1983. The pH varied from 6.9 to 7.7, and the dissolved

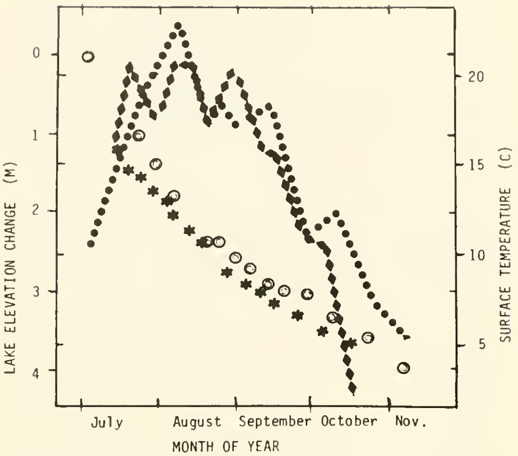

Fig. 1. Lake levels and surface temperature values for Desolation Lake for two wet years. Solid circles (1983) and diamonds (1984) depict the surface temperatures. Open circles (1983) and stars (1984) depict the lake level drop.

oxygen measured 6.6 mg/l. Nitrogen (greater than 60 ug N/l) was growth-limiting with respect to phosphorus (8–12 ug P/l) in the epilimnion. The hypolimnion contained more balanced amounts of phosphates and nitrogen and tended to have an increase in ammonia, carbon dioxide, phosphate, and many of the cations (zinc, iron, mercury, barium, and hexavalent chromium) and a decrease in oxygen (2.4 mg/l).

Desolation Pond is in the same basin as Desolation Lake and hence receives some of the snow from the same watershed. This pond is small, with a diameter of 20 m, a surface of less than 0.001 km^2, and during the wet year of 1984 a depth of 3 m. This pond dries in most years. Magnesium and calcium are the major cations and bicarbonate the major anion. Biological growth is limited with respect to nitrogen but not with respect to phosphorus.

Snow analysis in the Desolation Lake area indicated that this drainage basin received 52 kg sulfate, 4 kg nitrite N, and 41 kg nitrate N. The nitrogen value from atmospheric sources is equivalent to the nitrogen contribution of 100 sheep per 10 days in the basin (Darling 1973). This number of sheep in the basin is usually exceeded during most summers. Thus, both sheep and atmospheric sources of nitrogen can contribute significantly to the biological growth in Desolation Lake.

Thirteen of the 41 lakes examined in the central Wasatch mountains contained salamanders. Dog Lake was used in this study as an example of a seepage lake that did not experience a die-off. It is a seepage lake in Big Cottonwood Canyon with a surface area of approximately 0.007 km^2 within a drainage basin of 0.14 km^2. The lake is at 2,660 m elevation, has a depth of 2.4 m, and lowers in elevation during the summer approximately 0.6 m. Dog Lake has an abundance of aquatic insects such as Gerridae and Odonata and the leech *Batracobdella picta* (identified by Dr. D. J. Klemm). The abundance of macroinvertebrates in Dog Lake sharply contrasts with the paucity of macroinvertebrates in Desolation Lake.

Other seepage lakes that were observed included Red Pine Lake (elevation 2,684 m) and Shadow Lake (elevation 2,715 m) in the Weber River drainage and Lower Lake Solitude (elevation 2,684 m) in the Big Cottonwood drainage. Both Shadow Lake and Lower Lake Solitude were formed behind man-made dams and dried up in late summer. They also experienced salamander die-off, but since these lakes were very small, the die-off, although it may have been all-inclusive, did not involve large numbers. Only Lower Lake Solitude drainage was prohibited to the grazing of sheep. The drainage lakes did not experience any mass mortality.

Salamander populations in the high mountain lakes of Utah follow the life-history pattern described as "two size classes of larvae with metamorphosis occurring in the second warm season" (Sexton and Bizer 1978). Eggs are laid in these mountain lakes during July, although some lakes are utilized by breeding salamanders in August. Larval growth rates of 1.2 mm per day allow the young to reach the pretransformation snout-vent length of 55–70 mm by September (Fig. 2). Should the larvae reach a snout-vent length of about 40 mm by early August, they may metamorphose at that time, as indicated by Tanner et al. (1971). The aquatic young feed predominantly on crustaceans, including *Branchinecta paludosa*, *Gammarus lacustris*, and cladocerans. Transformed adult salamanders in the Desolation Lake region can arrive from populations derived from the drainage lakes of Willow Lake (2.4 km distant, ridgeline pass of 2,928 m, Big Cottonwood Creek drainage), Dog

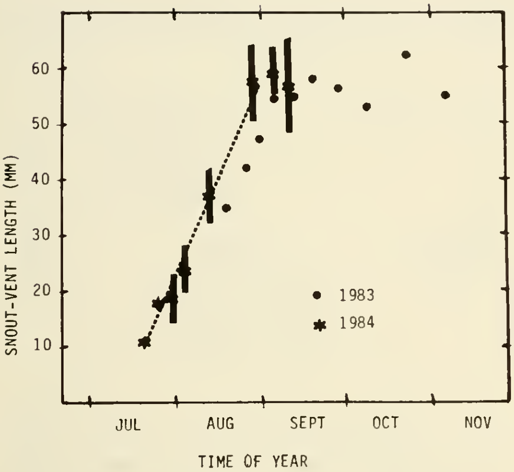

Fig. 2. Growth rates of aquatic larval salamanders in Desolation Lake. Stars represent average snout-vent length, with the bars representing one standard deviation for 1984. Solid circles represent average snout-vent length in 1983. The line represents a growth rate of 1.2 mm per day as determined by linear regression analysis from the data of 1984.

Lake (3.3 km distant, same tributary of Big Cottonwood Creek, no pass), and Red Pine Lake (0.8 km distant, ridgeline pass of 2,952 m, Weber River drainage).

RESULTS

Adult transformed salamanders die in July and August (Fig. 3). At least 33 (1982), 37 (1983), 22 (1984), 15 (1985), and 12 (1986) adults were observed dead in the water, on the shoreline, and under logs adjacent to the shoreline. The adults died in a rapid mode (1983), in a biphasic mode (1984), or in an extended mode (1985).

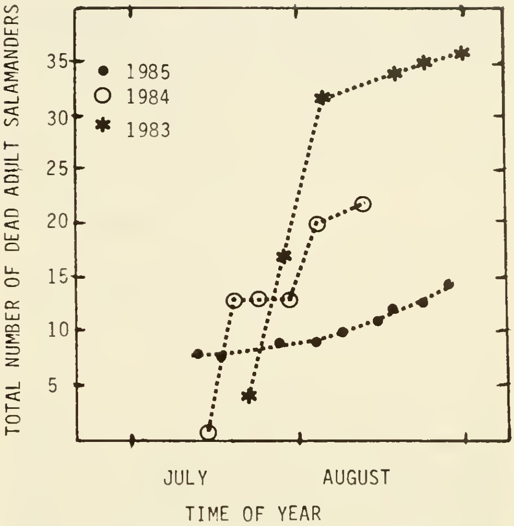

Fig. 3. Terrestrial adult mortality at Desolation Lake for three years.

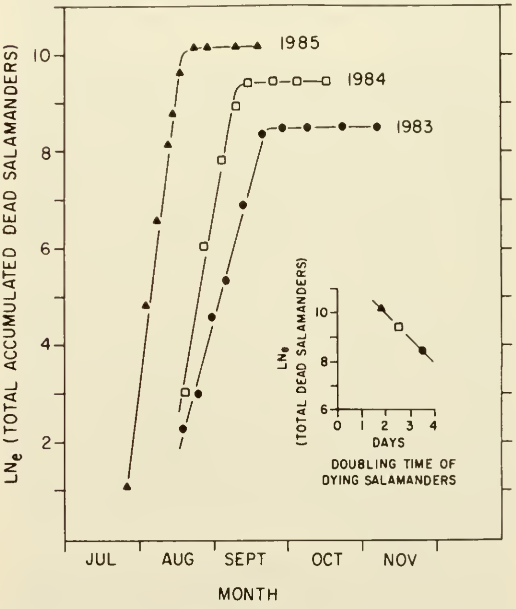

Fig. 4. The kinetics of the aquatic young salamander mortality in Desolation Lake for three years. The inset shows the relationship of the death rate to the total population.

The larval die-off at Desolation Lake started during mid-August 1983 and 1984 and the end of July 1985 (Fig. 4). A total of 4,949 (1983), 12,703 (1984), and 26,780 (1985) dead were counted. The mortality for these years was logarithmic, with its slope (determined by linear regression analysis of the accumulated sum of dead salamanders versus time) being 0.19 (1983), 0.28 (1984), and 0.40 (1985). Correlation coefficients were 0.99. The doubling time for the accumulation of dead salamanders was 3.6 (1983), 2.5 (1984), and 1.8 (1985) days. This doubling time was inversely proportional (slope −0.93) to the logarithm of the total dead salamanders (correlation coefficient 1.0) (Fig. 4 inset). The doubling of the mortality rate coincided with a fivefold increase in the total number of salamanders. Once the larval die-off started, the time for 50% of the salamanders to die was 13–16 days. In 1981 and 1982 the die-off occurred during this

TABLE 1. Experimental infection of healthy larval salamanders with *Acinetobacter calcoaceticus*, *Pseudomonas aeruginosa*, and *Escherichia coli; A. calcoaceticus* and *P. aeruginosa* were isolated from infected salamanders and *E. coli* from Desolation Lake. Approximately 300 million colony-forming bacteria were added to 8 liters of water in aquaria. Two salamanders were in each aquarium.

Aquarium No.	Inoculant	Disease developed	Inoculant recovered from salamander
1	None	No	Not applicable
		No	Not applicable
2	*A. calcoaceticus*	Yes (18 days)	Yes
		Yes (28 days)	Yes
3	*P. aeruginosa*	Yes (33 days)	Yes
		No	No
4	*E. coli*	No	No
		No	No

same period, but in 1980 it was completed by early August with much smaller young. The shift in the time of the die-off (Fig. 4) is related to the amount of winter (October to June) precipitation (correlation coefficient 0.86), which secondarily influences the depth of water in Desolation Lake and perhaps the time of year the adult salamanders travel to and breed in the lake.

To determine the etiology of the process, we searched for the proximate cause of the aquatic salamander deaths. Histological analysis indicated that salamander livers did not contain lesions attributable to organic compounds or heavy metals. Algal analysis indicated that the seepage lakes did not experience an algal bloom and that the lakes were oligotrophic during the summer. Water analysis did not turn up any unusual concentrations of heavy metals. Transferring salamanders from the lake in July and in August to aquaria showed that the July salamanders remained healthy throughout the summer and the August salamanders died at the same time as the lake population. This suggested an infectious etiology.

Microbiological evaluation disclosed that *Acinetobacter* could be isolated from the peritoneum, skin, and gills of recently expired specimens from Desolation Lake. We found only gram-positive bacteria (*Corynebacteria*, *Bacillus*, *Micrococci*, *Staphlococci*, and *Streptococci*) on the salamander gills and skin from specimens taken from three different Wasatch Mountain ponds and lakes where the salamanders completed their life cycle. Although some gram-positive bacteria could be isolated from ill salamanders, all the infected salamanders contained an *Acinetobacter* sp. on their skin and gills and only this species in the peritoneum. *Pseudomonas aeruginosa* could be isolated from some infected individuals along with *Acinetobacter*. *Acinetobacter* sp. was identified as *Acinetobacter calcoaceticus;* but since the taxonomy has been updated (Bouvet and Grimont 1986), the bacterium involved may be *A. haemolyticus* because the isolates from the salamanders and from Desolation Lake were strongly hemolytic and some isolates hydrolyzed gelatin. Furthermore, *Acinetobacter* sp. could not utilize nitrates in complex media.

Acinetobacter isolates from infected salamanders, upon inoculation of aquarium waters, did cause the mortality of salamanders (Table 1). *Acinetobacter* was then isolated from these diseased salamanders. Thus, our data satisfy Koch's postulates for the identification of *Acinetobacter* as the proximate cause of the aquatic salamander's deaths. *Pseudomonas* caused the disease in one of two animals by these same criteria. Because of its limited numbers, *Pseudomonas* may cause secondary infections in the diseased salamanders. *Escherichia coli* taken from Desolation Lake was ineffective in causing symptoms or mortality in aquaria. The infected salamanders from aquaria and from Desolation Lake at the time of death had red, swollen hind legs and vent region. The throat skin, abdominal skin, kidney, spleen, and stomach were major organs affected with diffuse hemorrhage—possibly due to the hemolytic nature of the *Acinetobacter* strain.

After establishing the proximate cause of the salamander deaths, we examined Desolation Lake for bacteria and algae. Bacterial analysis in Desolation Lake in August 1983 showed

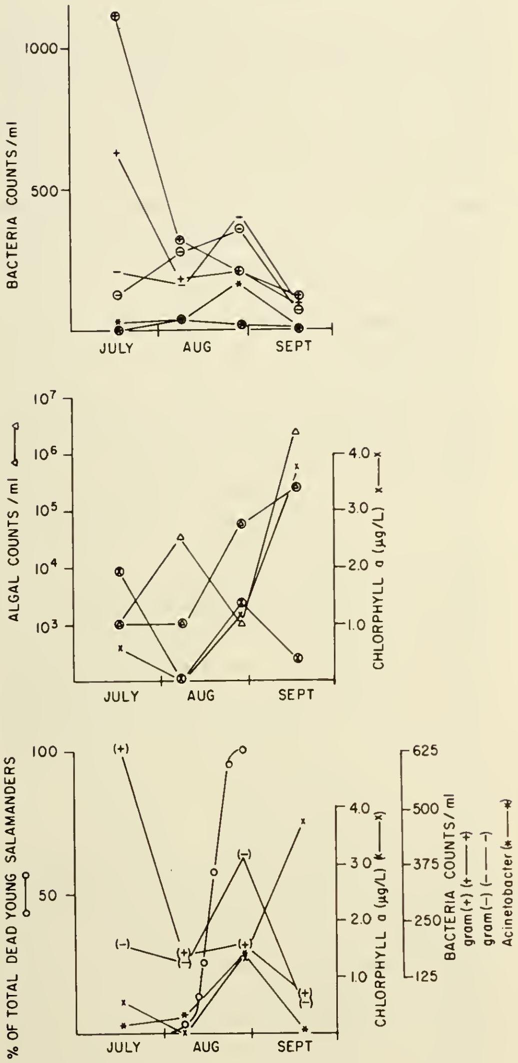

Fig. 5. Bottom: Desolation Lake salamander deaths in association with gram-positive (+) and gram negative (−) bacteria, *Acinetobacter* (star) levels, and chlorophyll *a* levels. Middle: Desolation and Dog lakes comparison (1985) of chlorophyll *a* and algal counts. Top: Desolation and Dog lakes comparison (1985) of gram-positive (+), gram-negative (−), and *Acinetobacter* (star) bacteria. The circled symbols represent Dog Lake. Algal counts of 10^3/ml were the minimum values detected. The difference between *Acinetobacter* levels and total gram-negative bacteria values is largely due to coliform bacteria.

gram-negative bacteria in the surface water (100/ml, only *Acinetobacter* sp.) and in the hypolimnion (greater than 1,000/ml with 100/ml as coliform and the remainder as *Acinetobacter*). In 1984 bacteria were undetected in the surface waters in our July sample (perhaps reflecting the snowmelt addition to the lake). The August sample was equally divided between gram-positive (190/ml) and gram-negative (220/ml). The September sample was entirely gram-negative (2,000/ml) and mostly *Acinetobacter*. Desolation Lake was largely void of bacteria in October.

In 1985 both Desolation and Dog lakes were examined at three-week intervals (Fig. 5). High numbers of gram-positive bacteria occurred in July and decreased in August and September. The gram-negative bacteria were present at low levels in July but peaked in late August at the end of the salamander die-off. By mid-September both Desolation and Dog lakes had a large decrease in gram-negative bacteria. Only in Desolation Lake did an *Acinetobacter* bloom occur, and this occurred at the same time as the salamander die-off. The remainder of the gram-negative bacteria in Dog and Desolation lakes were largely coliform bacteria.

Chlorophyll *a* and algal counts and identification showed that both Dog and Desolation lakes were oligotrophic at least until the end of summer (Fig. 5). An algal bloom might be considered as occurring in mid-September after the bacteria and salamander cycles occurred in Desolation Lake. This bloom was a result of the presence of the diatom *Cyclotella* (381 × 10^4/ml). In Dog Lake at this same time the diatom *Navicula* dominated (11.4 × 10^4/ml). Blue-green algae (*Anabaena*, *Oscillatoria*, and *Merismopedia*) occurred in both Dog and Desolation lakes, with *Chroococcus* occurring additionally in Desolation Lake. The two diatoms *Navicula* and *Cyclotella* occurred in both lakes. Green algae (*Chlamydemonas*-like) occurred in both Dog and Desolation lakes, with *Scenedesmus* occurring, in addition, in Desolation Lake and *Closterium* in Dog Lake. These studies indicate that the algal components of Desolation Lake did not contribute to the bacteria cycles in the lake or to the die-off of the salamanders.

Desolation Pond, adjacent to Desolation Lake, also experienced the salamander mass mortality. This pond is very small, a breeding ground for probably no more than one salamander pair. The die-off generally preceded the Desolation Lake mass mortality. In 1986 there was no die-off in Desolation Pond, while the die-off in Desolation Lake occurred in a typical manner.

DISCUSSION

Although the initial purpose of this study was to determine the proximate cause of the mass mortality in the salamander populations in Desolation Lake, observations of the bacteria, algae, and salamanders in seepage lakes did raise additional questions. Since these seepage lakes may all be nitrogen-limiting with respect to biological growth and this would extend previous observations for the region (Wurtsbaugh 1986), any addition of nitrogen, from grazing sheep in the watershed or from atmospheric sources, to the aquatic systems will alter the abundance and diversity of the microorganisms. To what extent this is occurring in Desolation Lake would require more studies as to the available nutrient and biological productivity at the bacteria level and at the aquatic insect level. With the average weight of an aquatic salamander in early autumn being 13.2 g (average snout-vent length of 67 mm), the total salamander productivity of Desolation Lake varied from 66 (1983) to 330 (1985) kg of wet weight. It would be interesting to note the biological productivity of salamanders in Desolation Lake without the external sources of nitrogen.

It is not known why *Acinetobacter* was dominant in Desolation Lake, nor is it known how the crustaceans in the lake influence the bacterial composition or how the aquatic salamanders affect the crustacean populations. It is known that salamanders affect the species and numbers of crustaceans in ponds (Dodson 1971, Giguére 1970). Since the crustaceans are large feeders of microorganisms, the salamanders may be contributing to their own deaths by allowing more bacteria to survive. Riemann (1985) noted that fish predation on zooplankton increased the bacterial numbers in a lake. Salamander predation on zooplankton should likewise allow for bacterial numbers to increase.

In Desolation Lake only large Dystiscidae have the capability to preying on the aquatic salamanders, but their numbers were low in comparison to other lakes in both the Wasatch and Uinta mountains. Most aquatic salamanders probably escape predation in Desolation Lake. In this study, then, the total dead aquatic salamanders for the year accounts for the total number of eggs laid. The ratio of total aquatic larvae to total adult (dead) salamanders varied from 137 (1983) to 577 (1984) and 1,912 (1985). If one assumes that an adult female lays from 250 to 350 eggs (Anderson et al. 1971) and that half of the dead adults were females, one can conclude that in 1983 all the adults died that bred in Desolation Lake. It is apparent that surplus adults can come from the region and adjacent lakes to breed in Desolation Lake.

Acinetobacter can act as a pathogen for other vertebrates. It is not known whether *Acinetobacter* was responsible for the deaths of other vertebrates at Desolation Lake. Besides the dead salamanders, 2 sheep, 2 mice, 2 ground squirrels, 1 porcupine, and 10 songbirds were found dead along the shore. Again, other lakes in these mountains did not reveal such numbers of dead mammals and birds; in fact, no dead mammals or birds could be found at the other lakes. The dead salamanders, birds, and mammals were fed upon by *Gammarus*, Trichoptera larvae, Dystiscidae, fungus, snails (Physidae), Hymenoptera, Diptera, and Coleoptera.

A proposed hypothesis to explain the seasonal salamander mortality states that the lake starts with fresh snow water in the epilimnion and old water from the previous year in the hypolimnion. The adult salamanders arrive at the lake in July to breed and feed in the bacteria-rich hypolimnion. While feeding, they become infected and die. The lake then experiences a gram-positive bloom and subsequent decline, attributed to the nitrate from snowmelt in the epilimnion. The lake level lowers and in this process the hypolimnion disappears. This allows the supply of gram-negative bacteria, including *Acinetobacter* which wintered in the hypolimnion, to bloom in the lake. At this time the aquatic young salamanders that have been growing all season long become infected and begin dying. At the peak of this salamander mortality, the gram-negative bacteria decline and subsequently the diatom bloom occurs. The timing of the seasonal cycles is related to the amount of winter precipitation, which directly affects the level of the lake in July.

CONCLUSIONS

We have described a recurrent annual salamander die-off attributed to *Acinetobacter* sp. in an oligotrophic lake. Not only was *Acinetobacter* sp. found to be the proximate cause by Koch's postulates, but it was also found to reach its greatest numbers in the lake at the peak of the mass mortality. Since the lake was found to be growth-limiting with respect to nitrogen, the addition of nitrogen from atmospheric sources and from sheep grazing in the watershed contributed to the abundance of bacteria and hence may be the ultimate perturbation of the lake system responsible for the salamander mass mortality. The seepage lakes with mass mortality had extensive lowering of the water levels. The seasonal timing of the biological cycles in the lake was correlated with the total snowfall.

This paper thus describes some of the biological properties of seepage lakes as well as some aspects of salamander biology as they relate to seepage lakes. It is apparent that such ecological disasters as salamander mass mortality can occur in aquatic systems without either acidification or eutrophication.

ACKNOWLEDGMENTS

We thank Dr. J. Harshbarger, Dr. R. I. Lynn, and M. A. Nielsen for their contributions in analysis. In addition, we thank M. Shaw (Wasatch National Forest, Salt Lake City), R. Radant (Utah Division of Wildlife Resources, Salt Lake City), and D. Schenck (Salt Lake City Water Department) for loan of water- and snow-sampling equipment; W. Hovingh, M. Hovingh, B. Coss, and B. Byrne for assistance in water sampling and counting dead salamanders; M. Hollander for assistance in snow sampling; Dr. D. J. Klemm (Environmental Monitoring and Support Laboratory, Environmental Protection Agency, Cincinnati, Ohio), Dr. G. M. Malacinski (Indiana University Axolotl Colony, Department of Biology, Bloomington, Indiana), and Dr. M. Piepkorn (Division of Dermatology, Department of Medicine, University of Utah Medical Center, Salt Lake City, Utah) for useful suggestions and directions.

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COMPARISON OF REGRESSION METHODS FOR BIOMASS ESTIMATION OF SAGEBRUSH AND BUNCHGRASS

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ABSTRACT.—Regression analyses for plant biomass estimation from physical measurements of individual plant dimensions that are nonlinear have generally used some form of the allometric equation. Use of this equation has most often involved logarithmic transformation of the variables (power regression). Transformation, however, introduces systematic bias into the analyses. Power regression was compared with a bias correction technique and with nonlinear regression for the prediction of the total foliage biomass (phytomass). Crown volumes of one sagebrush and one perennial grass species were used for these evaluations. The bias correction factor was uniformly applied to all the predicted values from power regression. Nonlinear regression avoided this bias by not requiring logarithmic transformation. It was also consistently less variable than either power regression or the correction factor method in estimating actual total phytomass by the allometric equation and equivalent or better in accuracy. The correction factor technique consistently gave the poorest predictions of the methods evaluated. Standard linear regression worked as well for the bunchgrass as the best method based on the allometric equation. Predictions were generally better when sample sizes used to derive the regression equations represented the range of plant size and variability in the data for which the phytomass was estimated.

Biologists often find it necessary to estimate the biomass or productivity of plant species on specific land areas (Payandeh 1981). Because biomass is difficult and expensive to collect, it is often estimated based on regression relationships between biomass and physical measurements of the individual plants (Tausch 1980, Tausch and Tueller 1988). Because these relationships are generally nonlinear, logarithmic transformation of the variables (power regression) has traditionally been used (Sprugel 1983). Transformation greatly simplifies the calculations because standard least-squares techniques for linear regression can be used. Systematic bias, however, is introduced into the results (Baskerville 1972, Payandeh 1981, Lee 1982, Sprugel 1983). Transformation also results in difficulties in evaluating the usual measures of goodness of fit (Payandeh 1981, Chiyenda and Kozak 1982).

Several techniques for correcting the bias introduced by transformation have been proposed, but two have been the most commonly applied. The first is an upward correction factor uniformly applied to all the predicted values from power regression (Lee 1982, Sprugel 1983). Second is the use of nonlinear regression not requiring logarithmic transformation of the data values (Payandeh 1981, Chiyenda and Kozak 1982). Any correction method should be simultaneously applied along with power regression. The results should be compared using independent data to test for the presence and correction of bias (Schlaegel 1981, Brand and Smith 1985).

Tests for bias correction have focused on the estimation of the weight of individual plants. When these tests are used by biologists, however, individual plant weights are often summed for determination of total plant weight on an area basis. The objectives of this study were to compare the standard power regression with corrected power and with nonlinear regression for estimating the total phytomass on sample sites. Total phytomass was estimated from crown volume for one sagebrush and one perennial grass species.

STUDY SITE DESCRIPTION

The study site is in a sagebrush-bunchgrass community located on the east flank of the Needle Range, southwestern Utah, at an elevation of 2,000 m. Topographically, the site is on a nearly level, occasionally dissected, relict fan-piedmont (Peterson 1981). The site slopes two degrees east-northeast. Low sagebrush (*Artemisia arbuscula* Nutt.) is the dominant shrub species, and squirreltail (*Sitanion*

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hystrix [Nutt.] J. G. Smith) is the most abundant bunchgrass. A soil profile on the site has a 24-cm deep A horizon over an argillic horizon. A calcium-carbonate cemented Bkm horizon starts at 38 cm and extends to 50 cm. The soil is a fine-loamy, mixed, frigid Xerollic Paleargid. There was no evidence of grazing at the time of sampling (Tausch 1980).

METHODS

Data-collection Methods

All data used were collected on a single sample area. This concentrated the analysis on variation among the individuals of each species on the site. The 8-m-wide by 20-m-long sample area was divided into 10 subplots, each 4 m on a side (16 m^2). The entire area was sampled in 1 × 2-m microplots with eight microplots per subplot. All low sagebrush and squirreltail bunchgrass plants with their trunk or basal area half or more in a microplot were sampled. Each shrub was measured for its longest crown diameter, the diameter perpendicular to the longest, and its crown height. Crown height was the longest vertical measure of the portion of the crown containing green foliage. The green foliage (phytomass) was individually collected for each shrub.

Squirreltail plants were individually measured for the longest diameter of their basal area, the diameter perpendicular to the longest, and culm height (Johnson et al. 1988). Grass phytomass was also collected by individual plant. A total of 474 low sagebrush and 122 squirreltail bunchgrass were sampled.

Crown volume for the shrubs was computed using the formula for one-half of an ellipsoid (Tausch 1980). Crown volume for the grass plants was computed with the formula for the volume of a cylinder using the basal area and the average culm height. This is the shape for bunchgrass that generally gives the best results (Johnson et al. 1988).

Analysis Methods

Nonlinear regression analyses were based on the allometric equation ($Y = aX^b$). For power regression both the X and Y variables were logarithmically transformed before analysis by linear regression (Payandeh 1981). Results from power regression were converted back to arithmetic form (antilogarithms) for most of the additional analyses. For nonlinear regression the parameters *a* and *b* were determined by an iterative technique. The correction factor (CF) for power regression was based on the square of the standard error of the estimate (SEE^2) computed from logarithmically transformed data (Sprugel 1983). The CF equaled the exponential of the SEE^2 divided by two ($CF = \exp[SEE^2/2]$). The CF, a number greater than 1.0, was then multiplied by all the estimated phytomass values before summing for the total phytomass.

Schlaegel (1981) recommended that several statistics be used when comparing biomass estimation equations. A coefficient of determination (r^2) and a standard error of the estimate were computed to compare the regression results. Also computed was a relative deviation. This was the difference between the estimated total phytomass and the actual total divided by actual total phytomass (%). Confidence limits for the relative deviations were computed using the chi-square technique from Freese (1960). The first two statistics permitted comparisons of the variability of the estimates by the different regression models. The last two were comparisons of how close the estimates were to the actual sampled total phytomass. All four statistics were computed from untransformed data as recommended by Payandeh (1981) and Brand and Smith (1985).

Ten data or equation sets were used to compute the crown volume to phytomass regression tests for low sagebrush. Data from 2 randomly selected subplots out of the 10 were combined for each equation set. Regression equations from each equation set were used to estimate total phytomass for the combination of the remaining 8 subplots (test sets) not used to derive each equation. Ten random groups of 4 subplots each were used in the equation sets to compute the crown volume to phytomass equations for the squirreltail bunchgrass. The resulting 10 regression equations were used to estimate the total phytomass for the combination of the 6 remaining subplots (test sets) associated with each of them. The random selections provided 10 estimates of total phytomass for each species using independent test sets (groups of 8 or 6 combined subplots, respectively).

TABLE 1. Sample size, maximum crown volume, and average foliage density in the plant crowns for *Artemisia arbuscula* in 10 equation sets (pairs of subplots randomly selected from 10) and in 10 test sets (combined 8 remaining subplots) associated with each equation set.

	Equation sets (2 subplots)			Test sets (8 subplots)		
Group number	Sample size	Maximum crown volume (dm^3)	Average foliage density (g/dm^3)	Sample size	Maximum crown volume (dm^3)	Average foliage density (g/dm^3)
1	46	29.15	4.50	428	65.60	4.98
2	63	65.60	4.57	411	37.90	4.97
3	110	30.63	5.34	364	65.60	4.81
4	100	14.93	5.44	374	65.60	4.81
5	138	30.63	5.54	336	65.60	4.73
6	118	16.89	5.83	356	65.60	4.69
7	117	65.60	5.15	357	37.90	4.81
8	50	65.60	4.68	424	37.90	4.94
9	121	29.15	4.94	353	65.60	4.89
10	77	37.90	4.34	397	65.60	5.08

Sample sizes were selected to be adequate for the site and to reflect the relative abundance of each species. Standard linear regression was also used with the bunchgrass data. Averages and standard deviations were computed for the r^2, standard error of the estimate, and the relative deviations for each combination of regression equation and species. Interpretation of the results included comparison of the densities of individual plants in the equation sets with the densities in the test sets used for each estimation. The ranges in crown volume and average foliage density in the plant crowns were also compared within and between the predicting and predicted data sets.

RESULTS AND DISCUSSION

Low sagebrush sample sizes for the 10 equation sets of random pairs of plots ranged from 46 to 138 individuals (Table 1). Sample sizes for the test sets of the combination of 8 remaining subplots associated with each equation set all exceeded 300 individuals. The largest maximum crown volume in the equation sets was about four times the smallest crown volume. In the test sets the smallest of the maximum crown volumes was more than half as large as the largest sampled. Maximum crown volume was less in the equation sets than in the test sets for 7 of the 10 pairs. Equation sets and test sets had a similar range in average foliage density in the plant crowns (Table 1). Squirreltail had sample sizes in the equation sets (4 plots) ranging from 33 to 66 individuals (Table 2). In the test sets sample sizes were generally, but not always, higher than the number of individuals in the equation sets. Maximum squirreltail crown volumes in both the equation sets and the test sets had similar 2:1 ranges in size. Equation set values were less than test set values in 6 of the 10 pairs. The range in foliage density was also similar between sets (Table 2). The r^2 values for the low sagebrush equation sets were usually less for nonlinear regression than for power regression results (Table 3). Coincidentally, standard error of the estimates for low sagebrush was consistently less for nonlinear regression. The value of regression parameter b was consistently higher for power regression than for nonlinear regression (Table 3).

Squirreltail bunchgrass regression results for the equation sets showed the same pattern as sagebrush but with a generally lower level of precision (Table 4). This appeared to be related to the lower sample size of the less abundant species. The relative increase in r^2 between power regression and nonlinear regression, however, was considerably larger than for sagebrush. The regression parameter b was larger for nonlinear regression than power regression, the opposite of the results for sagebrush. The regression parameter b for the nonlinear analysis results for squirreltail averaged very close to 1.0. Because of this, standard linear regression analysis was also used to derive prediction equations from the

TABLE 2. Sample size, maximum crown volume, and average foliage density in the plant crowns for *Sitanion hystrix* in 10 equation sets (groups of 4 subplots randomly selected from 10) and in 10 test sets (combined 6 remaining subplots) associated with each equation set.

	Equation sets (4 subplots)			Test sets (6 subplots)		
Group number	Sample size	Maximum crown volume (cm^3)	Average foliage density (g/dm^3)	Sample size	Maximum crown volume (cm^3)	Average foliage density (g/dm^3)
1	66	318.1	18.5	56	192.4	15.2
2	50	164.9	17.1	72	318.1	17.0
3	45	318.1	16.9	77	164.9	17.3
4	44	164.9	16.8	78	318.1	17.1
5	42	192.4	15.6	80	318.1	17.8
6	54	164.9	15.9	68	318.1	17.5
7	52	192.4	14.8	70	318.1	18.2
8	54	318.1	18.0	68	164.9	15.3
9	52	318.1	17.2	70	164.9	16.8
10	33	164.9	15.4	89	318.1	17.6

TABLE 3. *Artemisia arbuscula* crown volume to phytomass allometric regression analysis equations ($Y = aX^b$) by two methods for data for 10 equation sets, each composed of 2 randomly selected subplots.

	Power regression				Nonlinear regression			
Equation set number	a	b	r^2	Standard error (g)	a	b	r^2	Standard error (g)
1	0.0238	0.823	0.90	7.68	0.0939	0.670	0.96	5.22
2	0.0216	0.833	0.92	9.09	0.0454	0.751	0.94	7.43
3	0.0253	0.815	0.90	5.91	0.0336	0.786	0.90	5.87
4	0.0217	0.832	0.86	5.30	0.0543	0.725	0.87	5.06
5	0.0227	0.835	0.94	4.54	0.0378	0.776	0.95	4.27
6	0.0239	0.831	0.90	5.39	0.0261	0.821	0.90	5.39
7	0.0248	0.829	0.90	8.45	0.0606	0.726	0.96	5.51
8	0.0328	0.795	0.93	9.24	0.0664	0.716	0.96	7.10
9	0.0235	0.826	0.90	6.23	0.0757	0.691	0.94	4.78
10	0.0309	0.782	0.81	9.85	0.1039	0.651	0.84	9.12
mean	0.0251	0.820	0.90	7.17	0.0598	0.731	0.92	5.98
S.D.	0.0038	0.018	0.037	1.92	0.0257	0.053	0.042	1.48

10 equation sets (Table 5). Linear regression had an average r^2 and standard error very similar to nonlinear regression.

Low Sagebrush Predictions

Nonlinear regression averaged a higher r^2 and a lower standard error of the estimate than either power or corrected power regression when predicting the test sets (Table 6). The variabilities for the r^2 and standard error values were also less for nonlinear regression. Nonlinear regression had an average relative overestimate of actual total phytomass (+6.8%) that was about 75% larger than the results of power regression (+3.9%). Corrected power regression had an average relative overestimate over twice that of power regression. Where average foliage densities for the equation sets were greater than for the test sets, the predictions generally had larger total phytomass overestimates than when they were less. This was modified by differences in the range in crown volume between equation and test sets.

Although power regression had a closer estimate of actual low sagebrush phytomass, both the maximum underestimate (−9.6%) and overestimate (+14.2%) exceed the same values for nonlinear regression (−2.0% and +13.0%, respectively). Based on the methods of Freese (1960), power regression predicted total phytomass within 10.4% of the actual

TABLE 4. *Sitanion hystrix* crown volume to phytomass allometric regression analysis equations ($Y = aX^b$) by two methods for data for 10 equation sets, each composed of 4 randomly selected subplots.

	Power regression				Nonlinear regression			
Equation set number	a	b	r^2	Standard error (g)	a	b	r^2	Standard error (g)
1	0.0361	0.785	0.72	0.061	0.0157	1.03	0.90	0.036
2	0.0349	0.759	0.67	0.279	0.0245	0.89	0.73	0.250
3	0.0376	0.783	0.75	0.687	0.0100	1.10	0.89	0.447
4	0.0508	0.667	0.67	0.335	0.0164	0.99	0.80	0.259
5	0.0421	0.731	0.80	0.301	0.0239	0.89	0.86	0.257
6	0.0486	0.626	0.57	0.250	0.0235	0.87	0.67	0.216
7	0.0376	0.720	0.77	0.242	0.0221	0.88	0.84	0.202
8	0.0382	0.801	0.80	0.573	0.0162	1.02	0.90	0.416
9	0.0319	0.812	0.76	0.644	0.0114	1.08	0.91	0.400
10	0.0324	0.786	0.79	0.326	0.0206	0.93	0.85	0.277
mean	0.0390	0.747	0.73	0.370	0.0184	0.97	0.84	0.276
S.D.	0.0064	0.061	0.07	0.200	0.0053	0.09	0.006	0.121

TABLE 5. *Sitanion hystrix* crown volume to phytomass linear regression analysis equations ($Y = a + bX$) for data for 10 equation sets, each composed of 4 randomly selected subplots.

	Linear regression			
Equation set number	a	b	r^2	Standard error (g)
1	0.0070	0.0183	0.90	0.358
2	0.0733	0.0141	0.74	0.247
3	−0.0141	0.0171	0.89	0.455
4	0.0666	0.0145	0.81	0.254
5	0.0838	0.0134	0.86	0.254
6	0.0951	0.0115	0.70	0.207
7	0.0866	0.0118	0.85	0.195
8	0.0243	0.0175	0.90	0.416
9	−0.0133	0.0175	0.90	0.405
10	0.0454	0.0141	0.85	0.277
mean	0.0455	0.0150	0.84	0.307
S.D.	0.0418	0.0025	0.070	0.0942

at the 10% significance level. For nonlinear regression it was 11.4%, a difference much smaller than for the average of the overestimates. The greater precision of nonlinear regression resulted in estimates generally equivalent to those for power regression. The potential for extremes in over- or underprediction were also less for nonlinear regression. For corrected power regression, the confidence limit for the relative deviations was 14.0% of the actual at the 10% level of significance. The total range in the r^2 values for nonlinear regression (.84–.92) was just over half that of power regression (.78–.93) and less than half that of corrected power regression (.75–.94). Similar results occurred for the standard error of the estimate. The more representative the equation set was of the full site, the better the predictions generally were.

Squirreltail Bunchgrass Predictions

Test estimations of total squirreltail phytomass based on the allometric equation (Table 7) were more variable than those for low sagebrush (Table 6). Like the low sagebrush results, the least variability was with nonlinear regression. Unlike sagebrush, the best average accuracy for an average allometric estimate of total sampled squirreltail phytomass was with corrected power regression. Although the average for the relative deviations was the lowest for corrected power regression, its range of variation was greater than for either nonlinear regression or power regression. Nonlinear regression predicted total phytomass within 21.9% of the actual at the 10% level of significance. For corrected power regression it was 30.6% and for power regression it was 33.9% of the actual. The reduced variability for nonlinear regression resulted in the best predictions of squirreltail phytomass by the allometric equation. Differences in average foliage density between the equation sets and test sets (Table 2) were significantly correlated ($r = .94$, $P \leq .01$) with the relative deviations in the predictions (Table 7). When foliage density in the equation set was greater than or less than the test set, the test set was proportionally over- or

TABLE 6. Comparison of three allometric regression methods for determination of *Artemisia arbuscula* phytomass from crown volume. Equations were derived from combined data for equation sets of 2 random subplots (Table 3) out of 10 and used to estimate total phytomass for test sets of the combination of the remaining 8 plots.

Equation set number	Power regression			Corrected power regression			Nonlinear regression		
	r^2	Standard error (g)	Rel. dev. of total from act.	r^2	Standard error (g)	Rel. dev. of total from act.	r^2	Standard error (g)	Rel. dev. of total from act.
1	0.88	7.01	0.0067	0.87	7.38	0.0410	0.90	6.47	0.0661
2	0.87	6.82	−0.0060	0.84	7.73	0.0765	0.90	6.06	0.0331
3	0.89	7.08	0.0076	0.87	7.74	0.0577	0.86	8.01	0.1158
4	0.89	7.45	−0.0045	0.87	8.21	0.0513	0.92	6.45	−0.0198
5	0.82	9.28	0.0952	0.79	10.13	0.1357	0.88	7.63	0.0819
6	0.83	9.14	0.1183	0.79	10.13	0.1626	0.84	8.89	0.1198
7	0.78	8.85	0.1417	0.75	9.55	0.1785	0.87	6.87	0.1299
8	0.85	7.26	0.1007	0.83	7.80	0.1372	0.88	6.61	0.1350
9	0.88	7.59	0.0254	0.86	8.06	0.0596	0.90	6.67	0.0295
10	0.93	5.54	−0.0955	0.94	5.22	−0.0438	0.91	6.26	−0.0086
mean	0.86	7.60	0.0390	0.84	8.19	0.0863	0.89	6.99	0.0683
S.D.	0.041	1.174	0.0730	0.052	1.470	0.0676	0.0234	0.8983	0.0575

TABLE 7. Comparison of three allometric regression methods for determination of *Sitanion hystrix* phytomass from crown volume. Equations were derived from combined data for equation sets of 4 random subplots (Table 4) out of 10 and used to estimate total phytomass for test sets of the combination of the remaining 6 plots.

Equation set number	Power regression			Corrected power regression			Nonlinear regression		
	r^2	Standard error (g)	Rel. dev. of total from act.	r^2	Standard error (g)	Rel. dev. of total from act.	r^2	Standard error (g)	Rel. dev. of total from act.
1	0.83	0.264	−0.0213	0.81	0.282	0.1573	0.67	0.368	0.1698
2	0.64	0.692	−0.2898	0.73	0.597	−0.1649	0.83	0.474	−0.1075
3	0.72	0.278	−0.0250	0.72	0.280	0.1167	0.73	0.276	−0.1477
4	0.58	0.720	−0.2758	0.66	0.648	−0.1624	0.86	0.410	−0.0988
5	0.65	0.631	−0.2254	0.72	0.565	−0.1149	0.81	0.472	−0.1573
6	0.39	0.929	−0.4526	0.50	0.844	−0.3539	0.74	0.611	−0.2608
7	0.54	0.789	−0.3778	0.64	0.700	−0.2712	0.74	0.588	−0.2715
8	0.62	0.254	0.2090	0.47	0.300	0.3609	0.49	0.296	0.1263
9	0.73	0.289	−0.0827	0.74	0.285	0.0042	0.70	0.305	−0.0725
10	0.68	0.586	−0.2528	0.76	0.510	−0.1028	0.83	0.428	−0.1466
mean	0.64	0.543	−0.1794	0.67	0.501	−0.0531	0.74	0.423	−0.0967
S.D.	0.120	0.251	0.1978	0.111	0.204	0.2151	0.1090	0.117	0.1444

underestimated. Linear regression gave results for squirreltail better than any of the allometric-based methods (Table 8). It had the lowest average relative deviation and predicted total phytomass within 20.4% of actual at a 10% significance level. Squirreltail could also be analyzed by subdividing it into two parts. This would separate the nonlinear relationship of the smallest plants from the linear relationship of the larger plants. Each group could be analyzed separately to improve the estimation of the smallest plants.

CONCLUSIONS

Differences in total phytomass estimation between the evaluated regression methods stem from the usually skewed distribution of plant sizes on a site. The more abundant, smaller plants generally had denser crowns with more phytomass per unit of crown volume than the larger plants. Logarithmic transformation of the data for power regression decreased the values for larger plants more than for the smaller ones in a regression analysis. This gave the smaller plants with their denser crowns greater weight. In nonlinear regression the larger plants contributed to the analysis results more in proportion to their size. These differences were evident in the consistently larger values of the regression

TABLE 8. Linear regression prediction of *Sitanion hystrix* phytomass from crown volume. Equations were derived from combined data for equation sets of 4 random subplots (Table 5) out of 10 and used to estimate total phytomass for test sets of the combination of the remaining 6 plots.

	Linear regression		
Equation set number	r^2	Standard error (g)	Rel. dev. of total from act.
1	0.66	0.375	0.2150
2	0.85	0.443	−0.0737
3	0.73	0.275	−0.0377
4	0.86	0.419	−0.0594
5	0.83	0.449	0.1207
6	0.76	0.583	−0.2292
7	0.76	0.568	−0.2418
8	0.47	0.301	0.2116
9	0.69	0.310	0.0126
10	0.84	0.410	−0.1310
mean	0.74	0.410	−0.0213
S.D.	0.12	0.106	0.1632

parameter *b* in power regression results than in nonlinear regression results for sagebrush. Previous tests of the use of the correction factor (Baskerville 1972, Lee 1982) have been based on populations of individual plants that have generally been well distributed over the size range of the data. Greater numbers of smaller plants is more generally the rule in typical western shrub communities. When low sagebrush data were analyzed with power regression, the result was a general overestimation of the phytomass of the larger plants. This usually more than compensated for any underestimation of the smaller plants by logarithmic transformation bias. In closed-stand, pinyon-juniper woodlands the largest trees contributed more to the total phytomass on a site (Tausch and Tueller 1988) than they did for low sagebrush in this study. With the greater importance of the larger plants, the average overestimation of total phytomass by crown volume with power regression was 35.3%. Average overestimation from nonlinear regression was only 5.7%. The overestimation by power regression was increased, and by nonlinear regression decreased, compared to low sagebrush.

For squirreltail, the differences between power and nonlinear regression were the opposite of those for sagebrush. The lower values of regression parameter *b* and the associated greater curvature of the line occurred with power, rather than nonlinear, regression. The result from use of the power regression equation was, first, a small average underestimation of the smaller plants from logarithmic transformation bias. Second, there were larger underestimations of the larger plants from the dominance of the analyses by the smaller plants. Nonlinear regression eliminated the underestimation of the larger plants, but this was partially offset by an increased underestimation of some of the more numerous, smaller plants. An initial decline in the phytomass density with increasing crown volume in squirreltail occurred at a much smaller relative plant size than with sagebrush. The relationship was very nearly constant (linear) for most of the larger plants. Because the larger plants dominated the nonlinear regression analyses, the values of the parameter *b* were very close to 1.0 (Table 7), and linear regression worked as well (Table 8).

The general reduction in phytomass density with increasing plant size for both species could not be exactly matched by the mathematical capabilities of either allometric-based or linear equations. This resulted in either over- or underestimates for at least one part of the regression curve, depending on which regression method was used.

Bias from logarithmic transformation of the data values is a mathematical reality. It is, however, modified by other data characteristics. Particularly important are the differences in the pattern of phytomass density decline with increasing plant size, the distribution of plant sizes, and the sample size differences between data sets. The more the data set used to derive the estimation equations represented the data set being predicted, the better the results.

Nonlinear regression was the better choice for sagebrush despite the greater computation effort involved. It was nearly as accurate and had a much lower variability than the other two allometric-based methods. This lower variability appeared to be related to a better reflection of the crown phytomass density of the more dominant larger plants. The correction factor method should not be used for these types of data because it consistently had the poorest predictions.

ACKNOWLEDGMENTS

This research was done under a grant from the School of Graduate Studies, University of

Nevada at Reno. The author expresses his gratitude to Karen Chen for her help in processing and analyzing the data.

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LIST OF MONTANA SCOLYTIDAE (COLEOPTERA) AND NOTES ON NEW RECORDS

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and Michael A. Ivie[3]

ABSTRACT.—Listed are 96 species of Scolytidae (Coleoptera) from Montana. Eighteen species reported from Montana for the first time are: *Scierus pubescens* Swaine, *Hylastinus obscurus*(Marsham), *Hylesinus aculeatus* Say, *Hylesinus californicus* (Swaine), *Hylesinus criddlei* (Swaine), *Pseudohylesinus granulatus* (LeConte), *Dendroctonus punctatus* LeConte, *Phloeosinus hoferi* Blackman, *Phloeosinus pini* Swaine, *Carphoborus pinicolens* Wood, *Scolytus subscaber* LeConte, *Ips grandicollis* (Eichhoff), *Trypodendron betulae* Swaine, *Trypodendron retusum* (LeConte), *Trypophloeus populi* Hopkins, *Procryphalus mucronatus* (LeConte), *Pityophthorus alpinensis* G. Hopping, and *Gnathotrichus denticulatus* Blackman.

Montana, third largest of the contiguous 48 states, with elevations ranging from 555 to 3,901 m, is diverse ecologically and has flora representative of vaster areas around it. This circumstance has resulted in the occurrence of numerous scolytid species there. Ninety-six species are listed herein, including 18 species new to the state. Judging from published distributions of scolytids in Montana and from vegetation that grows in surrounding states and Canadian provinces, we believe additional species will doubtless be found in Montana.

Of the new records, only one species, *Hylastinus obscurus* (Marsham), is known not to be native to Montana. Another of the new Montana species, *Hylesinus aculeatus* Say, appears to be distributed throughout the range of green ash in the eastern half of Montana. This tree commonly exhibits progressive branch killing, which suggests to us that a fungus may be associated with the beetle. We recommend that this possibility be studied because of the importance of green ash as an ornamental tree.

Our source of published records of Montana scolytids is Wood (1982). Other records were obtained from the collections at Montana State University, USDA Forest Service Region One, Montana Division of Forestry, and by our collections.

Measurements of host trees are in metric units, as are distances from landmarks, although the latter are invariably in miles on labels of pinned museum specimens. Names of collectors are given as per labels or as stated in the literature. The numbers of known pinned adult specimens follow the collection data. Specimens deposited in the University of Idaho, William F. Barr Entomological Museum, are designated UI-WFBM. Other depositories are USDA Forest Service, Region One, Missoula (FS-R1); Montana State University, Bozeman (MSU); Montana Division of Forestry, Missoula (MDF); and State University of New York (SUNY).

SPECIES NEW TO MONTANA

Subfamily Hylesininae

Scierus pubescens Swaine

BIOLOGY.—Monogynous, unstudied. Infests *Abies lasiocarpa* and *Picea engelmannii* (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C.; USA: Alas., Colo., Ida. MONTANA: Bozeman Creek, 6,200′ (1,890 m), Gallatin Co., VIII–IX-1987, pitfall trap, D. L. Gustafson (1 MSU).

Hylastinus obscurus (Marsham)

BIOLOGY.—Monogynous. Infests the root crown of red clover in the spring. It is less common in other clovers. Overwinters as larvae or adults in the roots. There is one generation each year (Wood 1982).

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DISTRIBUTION AND NOTES.—EUROPE; NORTH AFRICA; CANADA: B.C., Ont.; USA: Calif., Conn., Ga., Ida., Ind., Md., Mass., Mich., N.H., N.J., N.Y., Ohio, Ore., Ut., Wash. MONTANA: Hamilton, Ravalli Co., 11-V-1936, Wilfred Shockley (1 MSU). Ronan, Lake Co., 8-VIII-1940, clover roots, H. B. Mills (2 MSU).

Hylesinus aculeatus Say

BIOLOGY.—Monogynous. Infests the bole and limbs of *Fraxinus* spp. Egg galleries are transverse and deeply etch the wood. Overwintering beetles evidently form feeding tunnels on green bark (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: Man., N.S., Ont., Que.; USA: Ark., Colo., Conn., D.C., Ill., Ind., Iowa, Kans., La., Me., Md., Mass., Mich., Miss., Nebr., N.H., N.J., N.Y., N.C., N.D., Ohio, Okla., Pa., S.C., S.D., Tenn., Tex., Va., W. Va. MONTANA: Conrad, Ponderosa Co., 7-XI-1985, *F. pennsylvanica*, J. Barringer (12 MSU). Cow Creek, Custer NF., Powder River Co., 31-V-1988, *F. pennsylvanica*, M. M. Furniss and S. J. Gast (21 UI-WFBM). Attacking broken-off trunk. Eight km N of Alzada, Carter Co., 1–VI-1988, *F. pennsylvanica*, M. M. Furniss and S. J. Gast (44 UI-WFBM). Infesting a felled 30-cm-diameter tree. Galleries throughout the stem and branches to a diameter of 2 cm. Galleries contained parents, eggs, and larvae.

Hylesinus californicus (Swaine)

BIOLOGY.—Monogynous. Evidently indistinguishable from *H. aculeatus* (Wood 1982).

DISTRIBUTION AND NOTES.—MEXICO: Chih.; USA: Ariz., Calif., Colo., N.M., N.D., Tex., Ut. MONTANA: Harlowton, Wheatland Co., 11-VII-1981, *Fraxinus* sp. (1 MSU). Bozeman, Gallatin Co., 1–10-VI-1988, funnel trap, D. L. Gustafson (1 MSU).

Hylesinus criddlei (Swaine)

BIOLOGY.—Monogynous, unstudied.

DISTRIBUTION AND NOTES.—CANADA: Man., Ont., Que., Sask.; USA: Colo., Iowa, Kans., Mich., Minn., N.D., S.D. MONTANA: Bozeman, Gallatin Co., VII–VIII-1977, sticky trap, S. Kohler (1 MDF). Bozeman, Gallatin Co., 1–30-IV-1988, funnel trap, D. L. Gustafson (1 MSU).

Pseudohylesinus granulatus (LeConte)

BIOLOGY.—Monogynous. Infests the base and roots of weakened true firs, Douglas-fir, and western hemlock. Egg galleries are short and transverse. A two-year life cycle is reported in northern Washington (Furniss and Carolin 1980).

DISTRIBUTION AND NOTES.—CANADA: B.C.; USA: Calif., Ida., Ore., Wash. MONTANA: Lake Co., 26-V-1936, R. D. Eichmann (1 MSU).

Dendroctonus punctatus LeConte

BIOLOGY.—Monogynous. Infests basal stem and roots of boreal spruces.

DISTRIBUTION AND NOTES: CANADA.—Alta., B.C., N.B., Newf., N.W.T., Ont., Que., Yukon; USA: Alas, Ida.[4], Penn., N.Y., W. Va. MONTANA: Glacier N.P., 11-VI-1986, *Picea glauca* x *engelmannii*, M. M. Furniss and J. B. Johnson (7 UI-WFBM). One gallery in a severely suppressed, 66-year-old tree of 17 cm basal diameter. Upper Red Rock Lake, Beaverhead Co., 29-V-1988, *P. glauca* x *engelmannii*, M. M. Furniss and S. J. Gast (15 UI-WFBM). Mature larvae at ground level in a 60-cm-diameter green tree; new adults in base of a 28-cm-diameter tree that had broken off at 1.5 m aboveground, one small branch with red foliage remained. Boulder Creek, Sweet Grass Co., 25-VII-1988, *Picea glauca* x *engelmannii*, M. M. Furniss and J. B. Johnson (59 UI-WFBM). Live female adults and young larvae collected near ground level in a live, suppressed, 90-year-old tree of 30 cm basal diameter and 14 m height.

Phloeosinus hoferi Blackman

BIOLOGY.—Monogynous. Unstudied. Infests bark of small branches and twigs of dying trees (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: B.C.; USA: Ariz., Calif., Colo., Ida., Nev., N.M., N.D., S.D., Tex., Ut., Wyo. MONTANA: 18 km SW of Alder, Madison Co., 7-IX-1978, *Juniperus scopulorum*, M. M. Furniss (11 ♀, 4 ♂ UI-WFBM). Infesting 5-cm-diameter stem. Thirteen km E of Decker, Bighorn Co., 31-V-1988, *Juniperus* sp., M. M. Furniss and

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[4] Unpublished record: Henrys Lake, Fremont Co., 22-VII-1988, *Picea glauca* x *P. engelmannii*, M. M. Furniss and J. B. Johnson (2 UI-WFBM). At ground level in a 25-cm-diameter, 8-m-tall, 35-year-old tree that had shed its dead foliage.

S. J. Gast (10 ♀, 10 ♂ UI-WFBM). Infesting faded 2.5-cm-diameter branch. Thirty-four km NE of Decker, Bighorn Co., 31-V-1988, *J. scopulorum*, M. M. Furniss and S. J. Gast (13 UI-WFBM). Infesting small branches of a felled 15-cm-diameter tree. Cow Creek, Custer NF, Powder River Co., 31-V-1988, *Juniperus* sp., M. M. Furniss and S. J. Gast (12 ♀, 13 ♂ UI-WFBM). Infesting lightly faded 1–1.5-cm-diameter branches on a 5-cm-diameter live tree. One and one-half km N of Tripoint Lookout, Custer NF, Carter Co., 2-VI-1988, *Juniperus* sp., M. M. Furniss and S. J. Gast (6 ♀, 5 ♂ UI-WFBM). Infesting 5-cm-diameter tree with faded top; galleries contained female beetles and eggs. Three km E of Reedpoint, Stillwater Co., 2-VI-1988, *J. scopulorum*, M. M. Furniss and S. J. Gast (11 UI-WFBM). Infesting 1–3-cm-diameter stem of a faded tree.

Phloeosinus pini Swaine

BIOLOGY.—Monogynous. Specimens have been reared from spruce branches and from a broken top of Jack pine (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: Man., N.W.T., Que.; USA: Alas., Ida.[5], Mich. MONTANA: Upper Red Rock Lake, Beaverhead Co., 29-V-1988, *Picea glauca* x *P. engelmannii*, M. M. Furniss and S. J. Gast (13 ♀, 12 ♂ UI-WFBM; 1 ♀, 1 ♂ FS-R1). Infesting 4-cm-diameter suppressed sapling. Much of the bark had been removed by woodpeckers.

Carphoborus pinicolens Wood

BIOLOGY.—Polygynous. Infests unthrifty or injured seedlings and broken branches of pines. Healthy seedlings on poor sites have also been killed by this beetle (Wood 1982).

DISTRIBUTION AND NOTES.—USA: Ariz., Calif., Colo., Ida., Nev., N.M., Ore., Ut., Wyo. MONTANA: Cardwell, Jefferson Co., 3-VI-1988, *Pinus flexilis*, M. M. Furniss and S. J. Gast (3 ♀, 2 ♂ UI-WFBM). Infesting 5-cm-diameter branches with red foliage; also present were *Pityophthorus* spp.

Subfamily Scolytinae

Scolytus subscaber LeConte

BIOLOGY.—Monogynous. Breeds in shaded-out branches and tops of suppressed or overmature trees. Egg galleries form a rounded E-shape and are typically impregnated with resin. Larval mines are hidden in phloem at first, then appear on the phloem inner face, extending in any direction (Wood 1982).

DISTRIBUTION AND NOTES.—CANADA: B.C.; USA: Calif., Ida., Ore., Wash. MONTANA: Roaring Lion Creek, 9 km S of Hamilton, Ravalli Co., 19-VII-1988, *Abies grandis*, M. M. Furniss and J. B. Johnson (1 ♀ UI-WFBM). Infesting a 3–4-cm-diameter bayonet-top of a 30-cm-diameter suppressed tree. Typical galleries also noted in 2½–4-cm-diameter broken branches on ground at this locality.

Ips grandicollis (Eichhoff)

BIOLOGY.—Breeds in slash, small branches, and vacant spaces among galleries of more aggressive bark beetles. Hosts include virtually all pines within its range. In the South, six or more generations occur per year; fewer probably occur in Montana.

DISTRIBUTION AND NOTES.—CANADA: Man., Ont., Que.; BAHAMAS; DOMINICAN REPUBLIC; GUATEMALA; HONDURAS; JAMAICA; NICARAGUA; USA: Great Lake states and New England to southern states, and isolated locations in Nebr. and S.D. MONTANA: North of Tripoint Lookout, Sioux Division, Custer NF, Carter Co., 2-VI-1988, *Pinus ponderosa*, M. M. Furniss and S. J. Gast (8 UI-WFBM, 2 SUNY). Infesting branches 2.5 cm diameter and smaller.

Trypodendron betulae Swaine

BIOLOGY.—Monogynous. Tunnels are constructed by females radially through bark into sapwood. The main tunnel branches at close intervals, left or right, in the same plane. Eggs are laid in niches oriented above and below the gallery. Larvae excavate short cradles in which they develop and feed on ambrosia fungus. Males are active in keeping the tunnels clean and aerated.

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C., Man., N.B., N.S., N.W.T., Ont., Que.; USA: Ida., Me., Mass., Minn., N.H., N.J., N.Y., S.D., Wisc. MONTANA: 16 km SE of Olney, Flathead Co., 10-VI-1986, *Alnus* sp., M. M. Furniss and J. B. Johnson (1 ♀,

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[5] Unpublished record: Henrys Lake, Fremont Co., 21-VII-1985, *Picea glauca* x *P. engelmannii* hybrid, M. M. Furniss and J. B. Johnson (4 UI-WFBM). Reared from lower branches of mature, standing tree that died in 1984.

1 ♂ UI-WFBM). Infesting 6-cm-diameter stem of a dying tree; a larva was present in one cradle.

Trypodendron retusum (LeConte)

Biology.—Monogynous. Infests stems of dying *Populus* spp; galleries are constructed radially at first, then follow growth rings transversely. Larvae develop in cradles aligned in single series above and below the transverse galleries. They feed on ambrosia fungus introduced by the parents (Wood 1982).

Distribution and notes.—Canada: Alta., B.C., Man., N.B., Ont., Que., Sask.; USA: Alas., Ariz., Calif., Colo., Conn., Ida., Mich., Minn., Nev., N.H., N.M., N.Y., Ore., Penn., S.D., Ut., Vt., Wash., W. Va., Wisc. Montana: Gallatin Co., 12-V-1942 (1 MSU). Eighteen km SW of Alder, Madison Co., IX-8-1978, *Populus tremuloides*, M. M. Furniss (1 UI-WFBM). Three km N Tripoint Lookout, Carter Co., 2-VI-1988, *P. tremuloides*, M. M. Furniss and S. J. Gast (4 UI-WFBM). Infesting stem of 9–12-cm-diameter recently dead tree.

Trypophloeus populi Hopkins

Biology.—The monogynous female excavates an irregular, 2-cm-long gallery just beneath the bark surface of stems or branches of standing, unhealthy, or dying trees. The galleries and larval mines do not show on the inner surface of the bark. One to one and one-half generations per year occur in Utah, overwintering as larvae; eggs are present in July (Petty 1977).

Distribution and notes.—Canada: Man., N.B., Sask.; USA: Ariz., Colo., Ida., Nev., Ut. Montana: About 5 km N Tripoint Lookout, Carter Co., 2-VI-1988, *Populus tremuloides*, M. M. Furniss and S. J. Gast (1 UI-WFBM). Sparsely infesting a limb of a standing dead tree.

Procryphalus mucronatus (LeConte)

Biology.—Monogynous. Prefers soft, fermenting, dead aspen bark; usually follows primary invasion by *Trypophloeus populi* Hopkins. The gallery is narrower and the bark overlying the gallery is thicker than that of *T. populi* and does not split as it does in the case of *T. populi*. One and one-half to two annual generations (Utah), overwintering as larvae and adults. Eggs appear in late May (Petty 1977).

Distribution and notes.—Canada: Alta., B.C.; USA: Alas., Colo., Ida., Nev., N.M., Ut. Montana: 18 km SW Alder, Madison Co., 8-IX-1978, *Populus tremuloides*, M. M. Furniss (7 UI-WFBM). About 5 km N Tripoint Lookout, Carter Co., 2-VI-1988, *P. tremuloides*, M. M. Furniss and S. J. Gast (2 UI-WFBM). Cadavers found in limb of dead mature aspen. Upper Red Rock Lake, Beaverhead Co., 20-VII-1988, *P. tremuloides*, M. M. Furniss and J. B. Johnson (4 UI-WFBM). Infesting stem of 30-cm-diameter tree. The last remaining live branch budded in spring 1988 and died. Adults had begun new galleries recently.

Pityophthorus alpinensis G. Hopping

Biology.—Polygynous. Infests broken branches and twigs, apparently one generation annually.

Distribution and notes.—Canada: Alta.; USA: Ida. Montana: Poorman Basin, 9 km NE Eureka, Lincoln Co., 21-VII-1988, *Larix lyallii*, S. J. Gast (2 ♀, 2 ♂ UI-WFBM; 2 ♀, 2 ♂ FS-R1). Lolo Peak, Missoula Co., 13-VIII-1988, *L. lyallii*, S. J. Gast and P. F. Kolb (2 ♀, 2 ♂ UI-WFBM; 2 ♀, 2 ♂ FS-R1). Trapper Peak, Ravalli Co., 2-X-1988, *L. lyallii*, S. J. Gast (5 ♀, 1 ♂ UI-WFBM; 6 ♀, 2 ♂ FS-R1). Infesting broken branches 0.5–4 cm diameter.

Gnathotrichus denticulatus Blackman

Biology.—Monogynous. Galleries are initiated by males and extend radially into xylem from which transverse tunnels follow the growth rings. Larvae develop in cradles excavated by them and feed primarily on ambrosia fungus introduced by the parents (Wood 1982).

Distribution and notes.—Mexico: Chih., D.F., Dgo., Guer., Mich., Pue., San Luis Potosi; USA: Ariz., Colo., N.M., S.D., Tex., Ut. Montana: Cow Creek Campground, Powder River Co., 1-VI-1988, *Pinus ponderosa*, M. M. Furniss and S. J. Gast (19 UI-WFBM). Infesting the base of a mature, lightning-struck tree with faded foliage. *Hylurgops s. subcostulatus* (Mannerheim), *Hylastes* sp., and *Orthotomicus caelatus* (Eichhoff) infesting the same tree. Lantis Springs Campground, Carter Co., 2-VI-1988, *P. ponderosa*, M. M. Furniss and S. J. Gast (1 UI-WFBM). Infesting 61-cm-diameter tree with red foliage. *Dendroctonus valens* LeConte larvae and *Ips calligraphus* (Germar) adults also present.

MONTANA SCOLYTIDAE

HYLESININAE
- **Hylastini**
  - *Scierus annectens* LeConte
  - *Scierus pubescens* Swaine
  - *Hylurgops porosus* (LeConte)
  - *Hylurgops reticulatus* Wood
  - *Hylurgops rugipennis pinifex* (Fitch)
  - *Hylurgops s. subcostulatus* (Mannerheim)
  - *Hylastes gracilis* LeConte
  - *Hylastes longicollis* Swaine
  - *Hylastes macer* LeConte
  - *Hylastes nigrinus* (Mannerheim)
  - *Hylastes ruber* Swaine
- **Hylesinini**
  - *Alniphagus aspericollis* (LeConte)
  - *Hylastinus obscurus* (Marsham)
  - *Hylesinus aculeatus* Say
  - *Hylesinus californicus* (Swaine)
  - *Hylesinus criddlei* (Swaine)
- **Tomicini**
  - *Xylechinus montanus* Blackman
  - *Pseudohylesinus granulatus* (LeConte)
  - *Pseudohylesinus n. nebulosus* (LeConte)
  - *Dendroctonus brevicomis* LeConte
  - *Dendroctonus murrayanae* Hopkins
  - *Dendroctonus ponderosae* Hopkins
  - *Dendroctonus pseudotsugae* Hopkins
  - *Dendroctonus punctatus* LeConte
  - *Dendroctonus rufipennis* (Kirby)
  - *Dendroctonus valens* LeConte
- **Phloeotribini**
  - *Phloeotribus lecontei* Schedl
- **Phloeosinini**
  - *Phloeosinus hoferi* Blackman
  - *Phloeosinus pini* Swaine
  - *Phloeosinus punctatus* LeConte
- **Hypoborini**
  - *Chaetophloeus heterodoxus* (Casey)
- **Polygraphini**
  - *Carphoborus carri* Swaine
  - *Carphoborus pinicolens* Wood
  - *Carphoborus ponderosae* Swaine
  - *Polygraphus rufipennis* (Kirby)

SCOLYTINAE
- **Scolytini**
  - *Scolytus laricis* Blackman
  - *Scolytus monticolae* Swaine
  - *Scolytus multistriatus* (Marsham)
  - *Scolytus opacus* Blackman
  - *Scolytus piceae* (Swaine)
  - *Scolytus rugulosus* (Müller)
  - *Scolytus subscaber* LeConte
  - *Scolytus tsugae* Swaine
  - *Scolytus unispinosus* LeConte
  - *Scolytus ventralis* LeConte
- **Crypturgini**
  - *Crypturgus borealis* Swaine
- **Dryocoetini**
  - *Dryocoetes affaber* (Mannerheim)
  - *Dryocoetes autographus* (Ratzeburg)
  - *Dryocoetes betulae* Hopkins
  - *Dryocoetes confusus* Swaine
  - *Dryocoetes sechelti* Swaine
- **Ipini**
  - *Pityogenes carinulatus* (LeConte)
  - *Pityogenes fossifrons* (LeConte)
  - *Pityogenes knechteli* Swaine
  - *Pityokteines lasiocarpi* (Swaine)
  - *Pityokteines minutus* (Swaine)
  - *Pityokteines ornatus* (Swaine)
  - *Orthotomicus caelatus* (Eichhoff)
  - *Ips b. borealis* Swaine
  - *Ips calligraphus* (Germar)
  - *Ips emarginatus* (LeConte)
  - *Ips grandicollis* (Eichhoff)
  - *Ips integer* (Eichhoff)
  - *Ips latidens* (LeConte)
  - *Ips mexicanus* (Hopkins)
  - *Ips montanus* (Eichhoff)
  - *Ips perterbatus* (Eichhoff)
  - *Ips pilifrons utahensis* Wood
  - *Ips pini* (Say)
  - *Ips p. plastographus* (LeConte)
  - *Ips tridens engelmanni* Swaine
  - *Ips woodi* Thatcher
- **Xyloterini**
  - *Trypodendron betulae* Swaine
  - *Trypodendron lineatum* (Olivier)
  - *Trypodendron retusum* (LeConte)
  - *Trypodendron rufitarsis* (Kirby)
- **Xyleborini**
  - *Xyleborus intrusus* Blandford
- **Cryphalini**
  - *Cryphalus r. ruficollis* Hopkins
  - *Trypophloeus populi* Hopkins
  - *Procryphalus mucronatus* (LeConte)
- **Corthylini**
  - *Conophthorus ponderosae* Hopkins
  - *Pityophthorus absonus* Blackman
  - *Pityophthorus alpinensis* G. Hopping
  - *Pityophthorus aquilus* Blackman
  - *Pityophthorus boycei* Swaine
  - *Pityophthorus confertus* Swaine
  - *Pityophthorus confinis* (LeConte)
  - *Pityophthorus digestus* (LeConte)
  - *Pityophthorus fuscus* Blackman
  - *Pityophthorus murrayanae* Blackman
  - *Pityophthorus nitidus* Swaine
  - *Pityophthorus pseudotsugae* Swaine
  - *Pityophthorus tuberculatus* Eichhoff
  - *Pityophthorus scalptus* Bright
  - *Gnathotrichus denticulatus* Blackman
  - *Gnathotrichus retusus* (LeConte)

ACKNOWLEDGMENTS

Dr. Stephen L. Wood, Brigham Young University, Provo, Utah, identified many of the scolytids mentioned herein and reviewed the manuscript. Jerald E. Dewey, USDA Forest Service, Missoula, Montana, also reviewed the manuscript and encouraged the project.

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FIRST NORTH AMERICAN RECORD OF *CICHLASOMA MANAGUENSE* (PISCES: CICHLIDAE)

Paul C. Marsh[1], Thomas A. Burke[2], Bruce D. DeMarais[3], and Michael E. Douglas[3]

ABSTRACT.—An established population of a neotropical cichlid fish, *Cichlasoma managuense*, was found in a spring pool in the Virgin River basin, Utah. Presence of this predatory species poses an additional threat to the native fish fauna of the Virgin River, which already has suffered multiple impacts of water development and introduced fishes.

Thirty-three *Cichlasoma managuense* (Günther) were seined from a thermal spring pool in the Virgin River basin of southwestern Utah on 13 September 1988. Specimens were 5.0–22.0 cm standard length (SL) and 4–278 gm (ASU 11861). The habitat, locally known as Boiler Spring, is adjacent to Interstate Highway 10 in the community of Washington (NW 1/4, S14, T42S, R15W, Washington County, Utah).

Cichlasoma managuense (guapote tigre or "jaguar guapote") is among the giant predatory cichlids or "true guapotes" of Central America and the Caribbean (Loiselle 1980). Its historic range includes Atlantic drainages of Central America from southern Costa Rica north to Río Patuco, Honduras (Miller 1966, 1976). The species has been introduced into Lake Amatitlan, Guatemala, the Río Chamelecon basin of northern Honduras, and lakes Liopango and Coatepeque, El Salvador (Bleicke 1972). Popular among aquarists, it was first imported to the United States in 1964 (Loiselle 1973, 1980). This represents the first documented feral occurrence of *C. managuense* in natural waters of North America.

The true guapotes are large, brightly colored, carnivorous cichlids ecologically equivalent to North American freshwater basses of the genus *Micropterus*. Guapotes are characterized by large, oblique, strongly protractile jaws, armed anteriorally with enlarged pseudocanine teeth. Adult *C. managuense* attain lengths of 40 (females) to 50 cm (males) SL. Natural habitat typically is turbid, slow-moving water over soft bottoms, although it is closely associated with rocky substrates in the Great Lakes of Nicaragua (McKaye 1977). Breeding occurs in a variety of places, from small tributaries of large rivers to flooded marshes (Bleicke 1972); fecundity is 50,000–60,000 ova/kg body weight (Villa 1982).

Boiler Spring is a natural limnocrene, which discharges about 0.015 m^3/sec through a modified outlet channel; mid-pool water temperature was 20 C in January. The spring pool was approximately circular (diameter ca 10 m), with sides sloping abruptly to a maximum depth of 1.5 m. Its bottom was centrally of sand and marginally of organic material. The site was shaded by nonnative salt cedar (*Tamarix* sp.) and palms (*Washingtonia filifera*), which ringed the pool. Introduced guppy (*Poecilia reticulata*, not collected) is the only other fish known from the pool (T. Hickman, personal communication). The main channel of the Virgin River is 2.75 km downflow, but it is unknown whether the two waters are confluent.

Southwestern springs have long been utilized as rearing or release sites for tropical and other nonnative fishes (Miller and Alcorn 1946, Hubbs and Deacon 1964, Courtenay and Deacon 1982, 1983, Deacon and Williams 1984, Courtenay et al. 1985). Many of these same habitats are (or were) occupied by native fishes, including isolated, endemic species or subspecies. Often, the result of nonnative fish introductions is extirpation of local populations. In some cases endemic species have been exterminated (Deacon et al. 1964, Minckley 1973, Courtenay et al. 1985), a result attributed primarily to direct predation (Meffe 1985). A similar relationship between native and exotic fishes has been demonstrated throughout the Southwest (Miller 1961, Minckley and Deacon 1968). It thus is alarming that highly predatory jaguar guapotes were established in a habitat within the Virgin River system, which contains an imperiled native fauna. We do not know if any native animals originally inhabited Boiler Spring.

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Six native fishes occupy the Virgin River basin: speckled dace (*Rhinichthys osculus yarrowi*), woundfin (*Plagopterus argentissimus*), Virgin River spinedace (*Lepidomeda m. mollispinis*), Virgin River roundtail chub (*Gila robusta seminuda*), flannelmouth sucker (*Catostomus latipinnis*), and desert sucker (*Pantosteus clarki*). The dace and two suckers are represented in main channel vs. springs and spring-fed tributaries by two or more distinct "forms" that are not yet taxonomically defined (W. L. Minckley, personal communication). Woundfin is federally listed as endangered, and the chub is a candidate for that category. Recent invasion of the Virgin River by red shiner (*Notropis lutrensis*) has resulted in dramatic declines in distribution and abundance of woundfin (Cross 1985, Deacon 1988). A suite of other nonnative fishes has been recorded from the system, representing additional threats to the native fauna.

Utah Division of Wildlife personnel attempted on 14 September 1988 to eliminate *C. managuense* from Boiler Spring (D. Knight, personal communication). Although several hundred were killed, treatment with both explosives and rotenone was unsuccessful in eradicating the animal (T. Burke, unpublished data). Moreover, local testimony indicated that *C. managuense* was present in other habitats, and at least one breeding population is established in a local private pond.

Cichlid fishes in general do not survive temperatures below about 10 C for more than a few days (Chervinski and Dor 1982). *Cichlasoma managuense* has likely been present in Boiler Spring for several years, with its overwintering enabled by warm temperatures in the pool. If access to the Virgin River were attained, the fish could spread in summer and survive cold seasons by occupying warm-water inflows that exist along the stream channel. Thermal tolerance data are wanting for *C. managuense*, but its establishment in relatively cool, high-elevation Lake Amatitlan, Guatemala, suggests that the species may have a lower lethal limit than other cichlids, a characteristic that enhances mobility and probability of establishment elsewhere. Presence of this cichlid is especially worrisome because of its predatory habit and the explosive reproductive potential afforded by its advanced parental care patterns (Breder and Rosen 1966, Loiselle 1982). Although impacts have not been demonstrated, potential exists for predation and other negative interactions between *C. managuense* and the native fauna. Attempts should thus be directed toward location and complete elimination of *C. managuense* from the system.

ACKNOWLEDGMENTS

We thank W. R. Courtenay for verifying identity of the animal and reviewing the manuscript. We also thank W. L. Minckley and S. P. Vives for reviews of the manuscript.

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CO-OCCUPANCY OF A DEN BY A PAIR OF GREAT BASIN BLACK BEARS

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Abstract.—An adult male and an adult female black bear (*Ursus americanus*) were found in the same den in the Carson Range of the Sierra Nevada in Nevada. Co-occupancy of dens is very rare, and such behavior has never been previously reported for adult bears of opposite sex.

Black bears are solitary animals except when mating, accompanied by cubs, or investigating areas of abundant, clumped food sources such as garbage dumps. They den almost exclusively as solitary individuals except for females accompanied by newborn cubs or yearlings (Beecham et al. 1983, Johnson and Pelton 1979, Lecount 1983, Rogers 1987, Schwartz et al. 1987, Tietje and Ruff 1980); however, Schwartz et al. (1987) reported unusual cases of co-occupancy of black bear dens. They found four instances of mothers denning with two- and four-year-old daughters and an additional case in which a mother and her yearling male denned with a two-year-old female that was not her offspring. Two reports of cannibalism on adult female bears by larger bears (Rogers 1987: 54, Tietje et al. 1987) suggest that group denning should be avoided, especially by adult members of the opposite sex. Adult males are usually much larger than adult females and thus more capable of cannibalism. In this report we describe co-occupancy of a den by an adult male and an adult female black bear.

As part of an ecological study of black bears in the Carson Range of the Sierra Nevada in Nevada, we entered dens in February and March 1988. On 21 February 1988 we found a four-year-old, 41-kg, transmitter-equipped female bear in the same den with an eight-year-old, 118-kg male (ages were determined by the cementum annuli technique [Stoneberg and Jonkel 1966]). Radio locations indicated that the female occupied the den all winter. There were no tracks in the snow to indicate that the male had recently entered the den, and deep snow (1–2 m) would have made travel to the den difficult after December 1987. Regardless of the date of entry by the male, follow-up radio locations indicated that the pair remained at the den site together until the end of April.

The den was under a large boulder at about 2,471 m in elevation and appeared to be partially excavated. There were two entrances, one open and the other blocked by snow. The floor of the den, approximately 4 m^2, was covered by a large amount of brush in which each bear had a separate depression or nest 80 cm apart.

It is unclear why such unusual behavior may occur. Energy conservation through heat transfer between den mates is one possibility, but Rogers (1987) found that bears did not effectively raise the temperature of their dens in Minnesota. Since the Great Basin bears were not touching, it is doubtful that a significant amount of heat was transferred between the two. Another possibility is that the female could have been in estrus, as noted in Rogers's (1987) study in Minnesota. Although we did not notice whether the female was in estrus when we entered the den, she was in estrus when recaptured on 16 June 1988, and on 17 June we saw her copulating with the male with whom she denned.

We thank the Nevada Department of Wildlife, Nevada Agricultural Experiment Station, and the Mzuri Wildlife Foundation for support of this study. Joel Berger, Carol Cunningham, and Linda Kerley made helpful comments on an earlier draft.

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HIGH-ELEVATION RECORDS FOR *NEOTOMA CINEREA* IN THE WHITE MOUNTAINS, CALIFORNIA

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ABSTRACT.—New records for bushy-tailed wood rat (*Neotoma cinerea*) on the White Mountains of eastern California increase the elevation from which this animal is known on the White Mountains, outside of human habitation, from 3,120 to 3,648 m. These records, coupled with archaeological data, suggest that the isolated bouldery outcrops occupied by bushy-tailed wood rats above timberline here are true habitat islands, occasionally colonized by dispersing individuals and characterized by frequent local extinction.

During the summer of 1984, a single bushy-tailed wood rat (*Neotoma cinerea*) was collected from the summit hut on White Mountain Peak (White Mountains, Inyo County, California) at an elevation of 4,342 m (Carey and Wehausen, in press). This record increased the maximum known elevation of *N. cinerea* in the White Mountains by 1,222 m and provided the highest known occurrence of this species in the Great Basin. However, because the animal was occupying a human structure, and because no records existed between 3,120 and 4,342 m, it is possible that the animal was transported to this elevation by people. In this paper we present new information on the distribution of *N. cinerea* in the higher elevations of the White Mountains and attempt to place the White Mountain Peak individual in local biogeographic perspective.

ARCHAEOLOGICAL RECORDS

Although human use of the alpine tundra zone of the central White Mountains extends back at least 5,000 years, the nature of human occupation here changed dramatically soon after A.D. 600, when a series of small village sites located at elevations between 3,150 and 3,850 m began to be occupied. A variety of dating techniques suggest that at least some of these sites were occupied by A.D. 660, and that at least some continued in use into early historic times (Bettinger and Oglesby 1985).

To date, the vertebrate faunas from 10 of these sites have been identified. The faunas are dominated by yellow-bellied marmots (*Marmota flaviventris*) and mountain sheep (*Ovis canadensis*), but a variety of smaller mammals are also represented. Six of the sites have provided the remains of *Neotoma cinerea* or *N.* cf. *cinerea* (Table 1). Specimens assigned to *N.* cf. *cinerea* cannot be identified to species with certainty, but they are much larger than corresponding elements of the desert wood rat, *N. lepida*, and there can be little doubt that they represent bushy-tailed wood rat. In addition, three of the sites have also provided teeth that can be securely identified as *Neotoma cinerea*.

MODERN RECORDS

The sites that provided these remains range from 3,150 to 3,560 m in elevation (see Table 1) and thus fall within the 1,222 m elevational gap in the currently known distribution of *N. cinerea* in the White Mountains. However, because these specimens are archaeological, it is possible that they represent either transport of the animals by people, as was common in the Great Basin ethnographically, or altered prehistoric distribution of wood rats in this area. To determine whether bushy-tailed wood rats exist here now, we sought *N. cinerea* sign adjacent to all 10 sites. We found such sign—cut vegetation, bone collections, rock-edge urine stains, and *Neotoma* scat—in the boulder accumulations adjacent to the following five sites:

1. *Crooked Forks*. The north-facing exposure of the rocky knob (elev. ca 3,158 m) above the Crooked Forks site, on Crooked Creek,

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TABLE 1. Modern and archaeological records for *Neotoma cinerea* in the White Mountains (NISP = number of identified specimens).

Village site	Elevation (m)	NISP	*Neotoma cinerea* present? Archaeological	Modern
Crooked Forks	3,150	950	yes (NISP, 9)	yes
Enfield	3,170	165	yes (NISP, 5)	yes
Corral Camp North	3,350	763	yes (NISP, 2)	no
Corral Camp South	3,350	791	no	yes
Midway	3,440	865	yes (NISP, 1)	no
Pressure Drop	3,460	92	no	yes
Raven Camp	3,460	720	yes (NISP, 1)	no
Rancho Deluxe	3,560	1,433	yes (NISP, 1)	no
Shooting Star	3,620	66	no	yes
12640	3,850	20	no	no

provided an accumulation of cut vegetation, skeletal material, and *Neotoma* scat that appeared fresh. The skeletal material included the remains of hares (*Lepus* sp.), Nuttall's cottontails (*Sylvilagus nuttallii*), *Marmota flaviventris*, meadow voles (*Microtus* sp.), and the proximal end of an *Ovis* second phalanx, the gracile nature of which suggests it is of domestic sheep (*Ovis aries*). In addition, this accumulation included five *Neotoma* mandibles, the measurements of four of which allow secure identification as *N. cinerea* (see Grayson 1983, 1985 for the use of mandibular and dental measurements to identify this animal). The dominant vegetation in this area includes sagebrush (*Artemisia* sp.), wax currant (*Ribes cereum*), occasional small limber pine (*Pinus flexilis*), and scattered to thick grasses.

2. *Enfield.* Located north of County Line Hill, the Enfield site sits below a small rock exposure, on the summit of which was found a small accumulation of *Neotoma* scat (elev. ca 3,190 m). This accumulation consisted of a small number of somewhat eroded pellets; no cut vegetation or other wood rat sign accompanied this material. The dominant vegetation on and immediately beneath this exposure includes rabbitbrush (*Chrysothamnus* sp.), *Artemisia* sp., and grasses.

3. *Corral Camp South.* Corral Camp South is in the upper reaches of the drainage of Cottonwood Creek; the rocky slope above this site provided a collection of *Neotoma* scat and a fragmentary *Neotoma* mandible (elev. ca 3,435 m). The dominant vegetation here includes bristlecone pine (*Pinus longaeva*), *Ribes cereum*, and scattered grasses.

4. *Pressure Drop.* Located west of Lamb Camp, the bouldery exposure (elev. ca 3,461 m) immediately above this site yielded a sparse collection of eroded *Neotoma* scat and a single distal right *Ovis* tibia, whose gracile nature again suggests domestic sheep. This scanty accumulation was on a west-facing slope, the dominant vegetation characterized by *Artemisia* sp., *Ribes cereum*, and scattered grasses.

5. *Shooting Star.* This site is located in the drainage of a small tributary of Cottonwood Creek approximately 1.2 km southeast of Barcroft Laboratory. The *Neotoma* accumulation found above this site consisted of scat, cut vegetation, and bones at an elevation of 3,633 m; typical *Neotoma* urine stains were found 15 m above this location. The bones collected from this midden included a cricetid femur, two pika (*Ochotona princeps*) mandibles, a *Marmota flaviventris* phalanx, a *Neotoma* lumbar vertebra, and the right maxilla of a juvenile domestic sheep. This material was found in a southwest-facing exposure behind a dense patch of *Ribes cereum;* other dominant plants in the vicinity of the midden include *Artemisia* sp. and scattered grasses.

These five records establish the presence of *Neotoma* some 530 m above the elevational limits documented by previous work in the area, though still 994 m beneath the White Mountain Peak summit record. While only the Crooked Forks midden specimens can be securely identified to species, the extreme elevation of the five accumulations leaves little doubt that all reflect the presence of *Neotoma cinerea*.

Because we did not trap, we do not know if any of these middens are still active. The association of the remains of domestic sheep with three of the accumulations, however, is significant. Although the associations may be accidental, the fact that three middens provided the remains of domestic sheep alongside other bones suggests that the sheep remains were collected by wood rats. If we accept these associations at face value, we can arrive at some indication of the age of the middens. Domestic sheep were introduced into the White Mountains during the 1890s. They began to be removed from the area in the 1930s, but scattered flocks remained as late as the 1950s (Wehausen 1986). Thus, at least three of the middens seem to have been active during the past 100 years, even if they are not active today.

CONCLUSIONS

Neotoma cinerea habitat is patchily distributed above timberline in the White Mountains. The bouldery exposures that provide cover for this animal may be separated from one another by hundreds of meters, the intervening expanses devoid of rocky cover and often nearly devoid of vegetation (Lloyd and Mitchell 1973). Although not all bouldery outcrops above timberline provide acceptable *Neotoma* shelter, some clearly do, and those that we have found with *Neotoma* sign are marked by vegetation that typically includes *Artemisia* sp., *Ribes cereum,* and scattered grasses. However, many outcrops that possess these attributes today show no sign of occupation by *Neotoma*. The archaeological site of Midway, for instance, is only 900 m from (and 120 m lower than) Shooting Star. The bouldery exposures above Midway are characterized by the same plants that characterize the slopes above Shooting Star; yet there is no evidence that *Neotoma cinerea* currently occupies the area. The species is, however, represented in the archaeological deposits of the site. Much the same can be said of Rancho Deluxe and Raven Camp: they are both adjacent to apparently appropriate habitat with no sign of contemporary *Neotoma*, but with *Neotoma* represented in the archaeological collections. We speculate that above-timberline, boulder-strewn exposures on the White Mountains often form true habitat islands for *N. cinerea*. These islands are occasionally colonized by dispersing bushy-tailed wood rats, with local extinction often following such colonization; the archaeological records from Midway and Raven Camp may, but do not necessarily, represent such extinctions. Escherich (1981) has noted the impressive dispersal abilities of *N. cinerea* and has noted as well that local populations of these animals commonly undergo extinction. Our data are fully consistent with his analysis.

Thus, new records for *N. cinerea* in the White Mountains increase the elevation from which this animal is known outside of human habitation from 3,120 to 3,648 m. Although elevations between 3,648 m and 4,342 m remain without records for this animal, we will not be surprised if dispersing individuals have occupied this zone as well. Even if the White Mountains Peak individual were transported by people, it arrived in much the same way as other bushy-tailed wood rats seem to have reached isolated patches of habitat above timberline here: dispersal across inhospitable areas.

ACKNOWLEDGMENTS

Funding for this work was provided by the National Science Foundation (BNS-8506972). We thank the White Mountain Research Station (especially R. L. Bettinger, D. L. Trydahl, and P. Trydahl) for field support, O. Pollack for plant identifications, C. Maser for verifying all identifications of *Neotoma* scat, and R. L. Bettinger, P. A. Kelly, and C. Maser for critical comments on the manuscript.

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OPPORTUNISTIC FORAGING BY THE KANGAROO RAT *DIPODOMYS DESERTI* STEPHENS (RODENTIA: HETEROMYIDAE)

Richard W. Rust[1]

ABSTRACT.—The kangaroo rat, *Dipodomys deserti* Stephens, was observed capturing and killing insects that were flying about an ultraviolet lamp. The white-lined sphinx moth, *Hyles lineata* (F.), and the carrot beetle, *Bothynus gibbosus* (DeGeer), were put into the cheek pouches and carried away from the collection area.

Heteromyid rodents are chiefly granivores whose foraging is enhanced by externally opening, paired, fur-lined cheek pouches (Hall 1981). Recent studies (Brown and Lieberman 1973, Reichman 1975, Brown et al. 1979, Bowers 1982, Price and Brown 1983) have demonstrated the use of seeds in the diet of heteromyid rodents. Schmidt-Nielsen (1964, 1979) showed that species of *Perognathus* and *Dipodomys* could be maintained in positive water balance in the laboratory on carbohydrate-rich, air-dried seeds as the sole energy and water source. However, Reichman (1975) found 15.5% of *Dipodomys merriami* Mearns and 16.2% of *Perognathus intermedium* Merriam diets to be insect. Harris (1986) found that *Microdipodops megacephalus* Merriam ate primarily arthropods. Jameson (1954) and Kritzman (1974) have shown Lepidoptera larvae to be important food for *Perognathus*.

Presented here are observations of carnivorous feeding in a large, seed-eating heteromyid, *Dipodomys deserti* Stephens. These observations were made over a four-night period in May 1987 at Eureka Sand Dune, Inyo County, California.

RESULTS

While I was collecting nocturnal insects with an ultraviolet lamp suspended over a collecting sheet, a *Dipodomys deserti* approached the sheet and began capturing, killing, and storing various beetles and moths in its cheek pouches (Fig. 1). During the first night (May 2), the kangaroo rat made several trips to the sheet and then finally stopped hunting, possibly due to the harassment of being photographed. The rat appeared the second night at approximately 20:30 hr and made eight undisturbed hunting sessions until the lamp was turned off at 23:00 hr.

The hunting sessions lasted an average of 7.1 ± 3.2 (SD) minutes (n = 8, range 3–12 minutes). Identifiable insects captured and removed were the white-lined sphinx moth, *Hyles lineata* (F.) (Lepidoptera: Sphingidae) and the carrot beetle, *Bothynus gibbosus* (DeGeer) (Coleoptera: Scarabaeidae). The rat took an average of 1.0 ± 0.7 (n = 8, range 0–2) white-lined sphinx moths and 1.6 ± 1.0 (n = 8, range 0–3) carrot beetles in the 2.5-hr hunting period. Many smaller beetles, mostly Scarabaeidae, and smaller moths were also captured and removed. The rat actively avoided all scorpions encountered near the collecting sheet.

Dipodomys deserti was adroit at handling and capturing moths and beetles. White-lined sphinx moths were even captured in the air as they approached the ultraviolet lamp. The rat removed their heads and wings (Fig. 1 foreground) before placing them in its cheek pouches. Beetles were bitten several times and then stored for transport.

The same spot was visited and the ultraviolet light was used five days later (May 8), but no *D. deserti* appeared during two nights of collecting. A *Dipodomys merriami* did approach the lamp and collecting sheet but did not respond to any of the insects present.

DISCUSSION

Were these observations a rare event or a regular feature of *Dipodomys deserti* feeding

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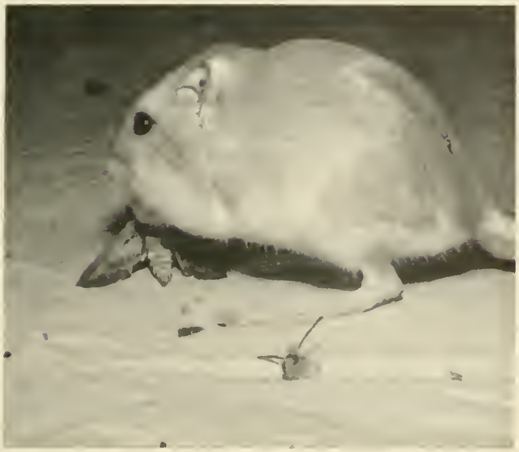

Fig. 1. *Dipodomys deserti* Stephens with a white-lined sphinx moth, *Hyles lineata* (F.), in its forepaws. Note the head of another white-lined sphinx moth on the sheet in the foreground.

behavior? Several lines of evidence suggest that it may not be that unusual for heteromyids to capture insects (Jameson 1954, Kritzman 1974, Reichman 1975, Harris 1986). The white-lined sphinx moth and carrot beetle are common throughout western deserts (Bechtel et al. 1982, Holland 1903, Powell and Hogue 1979). Both species fly at night in search of oviposition and feeding sites and would be present in the dune environment. The ease with which moths and beetles were captured and dispatched and with which scorpions were avoided suggests the kangaroo rat was familiar with these arthropods.

ACKNOWLEDGMENTS

I thank Colleen Cripps for commenting on the manuscript and my Biology 320 class for allowing me to make the undisturbed observations and for assisting me in recording captures.

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ADDITIONAL NEW SPECIES OF TERULIINE LEAFHOPPERS WITH KEY TO SPECIES (CICADELLIDAE: COELIDIINAE: TERULIINI)

M. W. Nielson[1]

ABSTRACT.—Five new species of teruliine leafhoppers from the Nearctic and Neotropical regions are described and illustrated. These include *Plapigella jessicae*, *Stalolidia crista*, and *Korsigianus christopheri* from Brazil; *Jikradia infula* from Mexico; and *Onblavia freytagi* from Venezuela. Revised keys to males of species of three genera are also given.

This paper is a continuation of studies of teruliine leafhoppers of the New World. Previous work on the genera *Plapigella* Nielson, *Stalolidia* Nielson, *Korsigianus* Nielson, *Jikradia* Nielson, and *Onblavia* Nielson are given elsewhere (Nielson 1979, 1983). Five new species are described and illustrated, one in each of the above genera, with a revised key to males of species of three genera.

Key to Males of *Plapigella*

1. Style tapered distally 2

— Style enlarged distally (Nielson 1979, Fig. 495) .... *elegans* (Spångberg)

2(1). Style with numerous setae distally 3

— Style without setae distally 4

3(2). Segment 10 with ventral process (Fig. 3) .... *jessicae*, n. sp.

— Segment 10 without ventral process (Nielson 1983, Fig. 19) .... *pilosa* Nielson

4(2). Aedeagus with short, stubby setae about middle of shaft (Nielson 1979, Fig. 500). . . *persoluta* Nielson

— Aedeagus with short to long, very fine setae subdistally (Nielson 1979, Fig. 505) .... *multispinosa* Nielson

Plapigella jessicae, n. sp.

Figs. 1–9

LENGTH.—Male 6.70–6.90 mm, female 7.60 mm.

General color ochraceous with fuscous transverse bands on forewings. Crown yellow in male, deep ochre in female; eyes rufous; pronotum rufous to light ochre; scutellum light ochre; forewings with 2 broad, fuscous, transverse bands, bands with small to large, light yellow to light ochraceous spots; face light yellow to light ochre. Similar to *pilosa* in some genital characters and can be separated by the broad ventral process of segment 10.

Head very broad and short, slightly narrower than pronotum (Fig. 1); crown narrow, width less than width of eyes, slightly produced beyond anterior margin of eyes, disc foveate; eyes large, semiglobular; pronotum very short, median length less than median length of crown, surface with numerous bullae; scutellum moderately large, length greater than median length of crown; forewings and venation typical; clypeus long and narrow, with prominent, median, longitudinal carina; clypellus long and narrow, lateral margins expanded distally (Fig. 2).

MALE.—Pygofer in lateral view with long, robust caudodorsal lobe; segment 10 with short, broad, ventral process, toothed distally (Fig. 3); aedeagus asymmetrical, somewhat tubular, with apex curved dorsally in lateral view (Fig. 5), and with numerous short to long, stout setae on ventral margin from near middle to near apex of shaft (Figs. 4, 5); style long and narrow in distal 3/4, slightly bulbous subapically, with short distal spine and numerous microsetae subapically (Figs. 6, 7); plate long and narrow, with few setae distally (Fig. 8).

FEMALE.—Seventh sternum large, about 2.5 times as long as preceeding segment, caudal margin broadly excavated on either side of middle and with median, short, toothed projection (Fig. 9).

HOLOTYPE (male).—BRAZIL: Amazonas, Manaus, 60 km N Reserva Campinas, 14.I.1977, Norman D. Penny (INPA). Allotype (female): BRAZIL: Est. Aml., Km 134,

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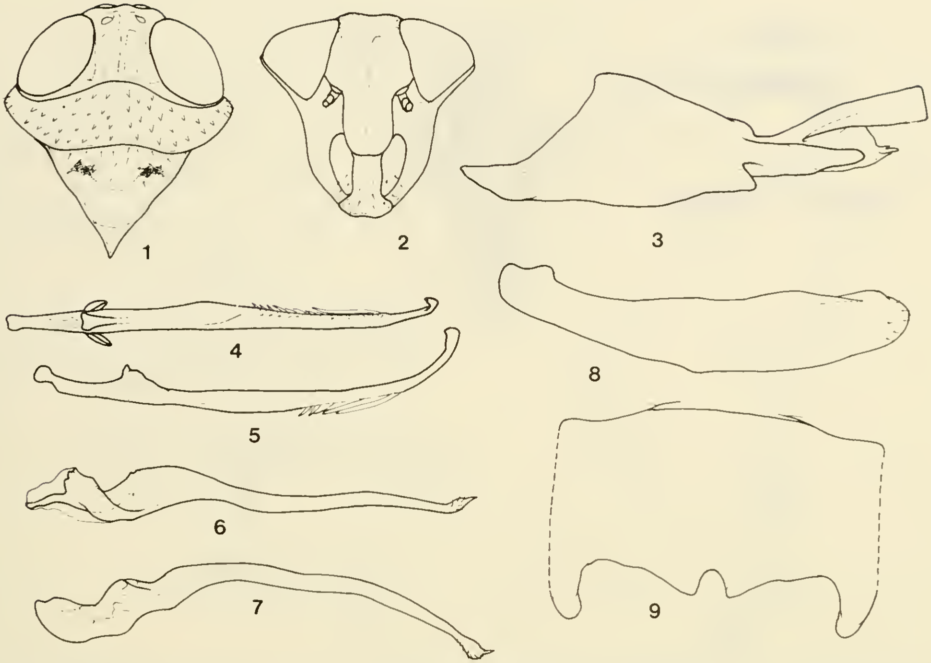


Figs. 1–9. *Plapigella jessicae*, n. sp.: 1, head, pronotum, and scutellum, dorsal view; 2, face, ventral view; 3, male pygofer, lateral view; 4, aedeagus, dorsal view; 5, aedeagus, lateral view; 6, style, dorsal view; 7, style, lateral view; 8, plate, ventral view; 9, female seventh sternum, ventral view.

En.(?), Am. (Amazonas), 10.VIII.1968, E. V. Silva & A. Faustino, #2854 (INPA). Paratypes (1 male): Manaus, Amazonas, 7.XII.1977, B. C. Ratcliffe (author's collection), 1 specimen (abdomen missing), Labesa (?), Amazonas, 27.V.1963, Dorqueira Antonio, #2416 (INPA).

REMARKS.—This species can be distinguished from all other known species of *Plapigella* by the prominent ventral process on segment 10. This species is named for my granddaughter, Jessica Larsen.

Key to Males of *Korsigianus*

1. Pygofer in lateral view with large, bladelike caudoventral process (Fig. 12); style very short and broad, without processes (Figs. 15, 16) .... *christopheri*, n. sp.

— Pygofer in lateral view with very narrow, spinelike caudoventral process (Nielson 1979, Fig. 1268); style very long and narrow, with lateral process (Nielson 1979, Fig. 1270)..................................... *exoptatus* (Walker)

Korsigianus christopheri, n. sp.

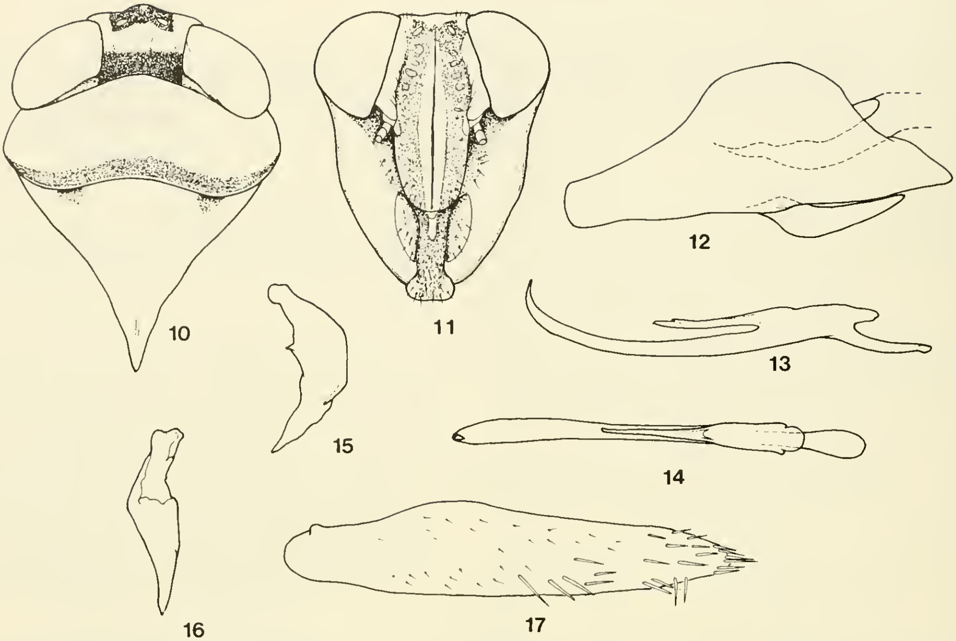
Figs. 10–17

LENGTH.—Male 9.00 mm.

General color light tannish to yellow with fuscous to black markings. Crown pale yellow with a black rectangular marking basally and black marking in middle of apex, continuing as parallel, black, longitudinal stripes on clypeus and clypellus; pronotum deep yellow except for narrow, transverse, black band basally; scutellum deep tannish suffused with light fuscous markings along anterior margin; forewings translucent except for transverse, subdistal, fuscous band and distal fuscous apex, veins black. This species is remarkably similar to *exoptata* in color patterns but can be readily distinguished by genital characters described below.

Head broad and short, narrower than pronotum (Fig. 10); crown broad, about as wide as width of eyes, lateral margins slightly convergent basally; eyes large, semiglobular; pronotum large, median length about twice median length of crown; scutellum very large, median length greater than median length of pronotum; forewings and venation typical; clypeus long and narrow, with prominent, median, longitudinal carina; clypellus long and narrow, constricted subapically (Fig. 11).

MALE.—Pygofer in lateral view with broad, bladelike caudoventral process (Fig. 12); aedeagus slightly asymmetrical, with long



Figs. 10–17. *Korsigianus christopheri*, n. sp.: 10, head, pronotum, and scutellum, dorsal view; 11, face, ventral view; 12, male pygofer, lateral view; 13, aedeagus, lateral view; 14, aedeagus, dorsal view; 15, style, lateral view; 16, style, dorsal view; 17, plate, ventral view.

ventral process curved dorsad in lateral view (Fig. 13), aedeagal shaft dorsal, reaching to about midlength of ventral process, gonopore subapical (Figs. 13, 14); style short, triangulate (Figs. 15, 16); plate long, narrow, with numerous setae on surface (Fig. 17).

FEMALE.—Unknown.

HOLOTYPE (male).—BRAZIL: Reserva Ducke, Manaus, Amazonas, 29.XII.1976, N. D. Penny (INPA).

REMARKS.—Two species are known in the genus. From *exoptata*, which is known from Peru and Guyana, *christopheri* can be easily distinguished by the very short, triangulate style and the broad, bladelike caudoventral process of the pygofer. I name this species for my grandson, Christopher Scott Checketts.

Jikradia infula, n. sp.

Figs. 18–23

LENGTH.—Male 8.00 mm.

General color dark fuscous with 2 broad, ochraceous, transverse bands on forewings; crown deep ochraceous; eyes rufous; pronotum and scutellum black; clypeus ochraceous in anterior half, black posteriorly. Similar to *olitoria* (Say) in male genital characters but with distinctive color patterns.

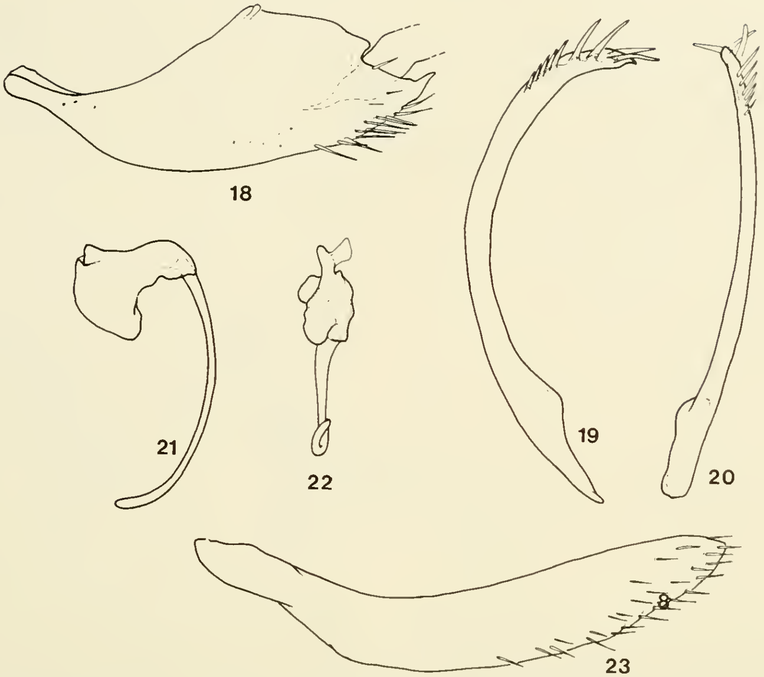
Head distinctly narrower than pronotum; crown broad, width greater than width of eyes, produced slightly beyond anterior margin of eyes; eyes large, semiglobular; pronotum moderately large, median length greater than median length of crown; scutellum with median length much greater than median length of pronotum; forewings and venation typical; clypeus long and narrow, with prominent, median, longitudinal carina; clypellus narrow, lateral margins expanded distally.

MALE.—Pygofer in lateral view with short caudodorsal lobe (Fig. 18); aedeagus asymmetrical, long, tubular, and curved dorsally in lateral view (Fig. 19), with several short to long, stout setae near ventral margin in distal 1/5 (Figs. 19, 20), gonopore near apex; style with long, narrow apophysis (Figs. 21, 22); plate long and narrow, with numerous short setae in distal half (Fig. 23).

FEMALE.—Unknown.

HOLOTYPE (male).—MEXICO: Guerrero, 22 mi N Chilpancingo, 24.VIII.1958, H. F. Howden (CNC).

REMARKS.—This species has remarkable color patterns unlike any other known species of *Jikradia*. The two broad, yellow to



Figs. 18–23. *Jikradia infula*, n. sp.: 18, male pygofer, lateral view; 19, aedeagus, lateral view; 20, aedeagus, ventral view; 21, style, lateral view; 22, style, dorsal view; 23, plate, ventral view.

ochraceous, transverse bands on the forewings will readily distinguish it from all other species. The size and arrangement of the aedeagal setae will also separate the species from *olitoria*, its nearest relative.

Key to Males of *Onblavia*

1. General color flavous; aedeagus with numerous long setae along middle of shaft (Nielson 1979, Fig. 1242) . . . . *flavocapitata* Nielson

— General color black, aedeagus with 2 long setae subapically (Figs. 25, 26) . . . . *freytagi*, n. sp.

Onblavia freytagi, n. sp.

Figs. 24–29

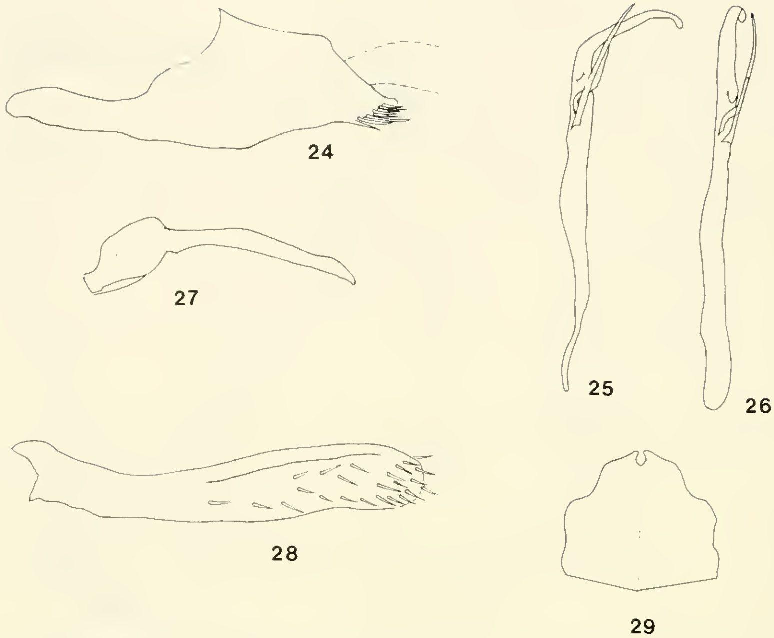
LENGTH.—Male 7.20 mm, female 8.00–8.30 mm.

General color black except for yellow to ochraceous along costa of forewings and most of face in female, more deeply marked in male; eyes rufous. Similar to *flavocapitata* but with different color and male aedeagal structures.

Head distinctly narrower than pronotum, anterior margin rounded; crown broad, about as wide as width of eyes, lateral margins slightly convergent basally, slightly produced beyond anterior margin of eyes; eyes large, subglobular; pronotum short, median length less than median length of crown; scutellum large, length to basal angle much greater than median length of pronotum; forewings and venation typical; clypeus long and somewhat broad, with median, longitudinal carina; clypellus long and narrow, apex expanded laterally.

MALE.—Pygofer in lateral view with small lobe arising mesally on caudodorsal margin (Fig. 24); aedeagus asymmetrical, long, tubular, gradually attenuated toward apex, abruptly curved dorsally in distal 1/3 and again at apex in lateral view (Fig. 25), with 2 long, setaelike spines of unequal length distad of middle on ventral margin of shaft, spines directed distally, gonopore lateral near base of spines (Figs. 25, 26); style with long, nearly flat apophysis (Figs. 27); plate long and very narrow, with numerous coarse setae in distal half (Fig. 28).

FEMALE.—Seventh sternum large, about 3 times as long as preceeding segment, caudal margin produced in middle third, notched distally (Fig. 29).



Figs. 24–29. *Onblavia freytagi*, n. sp.: 24, male pygofer, lateral view; 25, aedeagus, lateral view; 26, aedeagus, ventral view; 27, style, lateral view; 28, plate, ventral view; 29, female seventh sternum, ventral view.

HOLOTYPE (male).—VENEZUELA: Laguna de los Cedros, near Bocund-Trujillo, 1,200 m, 12.VI.1986, P. H. Freytag & M. A. Gaini (UKL). Paratypes (3 females), same data as holotype (UKL, author's collection).

REMARKS.—Two known species in the genus occur only in Venezuela. From *flavocapitata*, to which it is similar in aedeagal characters, *freytagi* can be separated by the presence of 2 setaelike spines distad of middle of shaft. I dedicate this species to Dr. Paul H. Freytag, University of Kentucky, for his fine work on Neotropical leafhoppers and for his part in collecting material of this species.

Stalolidia crista, n. sp.

Figs. 30–36

LENGTH.—Male 8.90–9.00 mm.

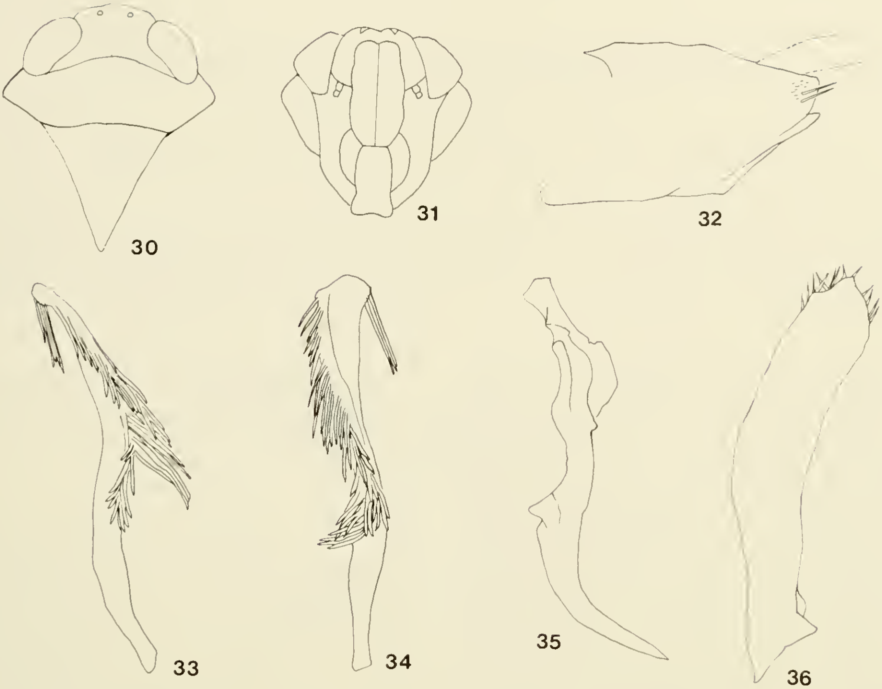
General color deep fuscous with 2 broad, translucent, irregular, transverse bands on forewings, veins with small yellow spots, small translucent spots in apical 1/3; crown light tan; eyes rufous.

Head distinctly narrower than pronotum; crown broad, subquadrate; eyes large, elongate-ovoid (Fig. 30); pronotum large, anterior margin broadly rounded; scutellum very large; forewing broad, 5 apical cells and 3 anteapical cells present, outer one closed, appendix well developed; clypeus long and moderately broad, with prominent, median, longitudinal carina (Fig. 31); clypellus long, slightly tumid basally.

MALE.—Pygofer with short, broad, caudoventral lobe, small mesal lobe on caudodorsal margin (Fig. 32); segment 10 moderately long and broad, without ventral processes; aedeagus asymmetrical, very long, sinuate, somewhat compressed dorsoventrally at apical 1/5 in lateral view, with numerous long setae arranged in a sinuate row basad of middle of shaft near lateral margin and extending to apex, several setae on opposite lateral margin near apex, setae directed laterobasally (Figs. 33, 34), gonopore cryptic near middle of shaft on lateral margin; style very long, broadly curved, and pointed apically in lateral view, with short, triangulate lobe near middle of inner margin (Fig. 35); plate long, narrow, acutely angled distally, with few fine setae distally (Fig. 36).

FEMALE.—Unknown.

HOLOTYPE (male).—BRAZIL: Rondonia, 7 km E Costa Marques, 11–13.IV.1987, Malaise trap, T. Klein (OSU). Paratype (1 male),



Figs. 30–36. *Stalolidia crista*, n. sp.: 30, head, pronotum, and scutellum, dorsal view; 31, face, ventral view; 32, male pygofer, lateral view; 33, aedeagus, lateral view; 34, aedeagus, ventral view; 35, style, lateral view; 36, plate, ventral view.

same data as holotype except 30.VII.1988 (author's collection).

REMARKS.—This species keys to couplet 7 and no further in Nielson (1979). It is similar to *stali* Nielson in male genital characters but can be distinguished by the narrower caudal margin of the pygofer, broader aedeagus at distal 1/3 in ventral view, triangulate lobe on the inner margin of style, and the uninterrupted row of setae on the aedeagal shaft. Twelve species are now known in the genus, all from South America.

NOTES.—The Malaise trap used by various collectors for collecting insects in the Neotropical region has been very useful for capturing males of coelidiine leafhoppers. Among 12 specimens collected in Brazil by Terry Klein, 11 were males, representing 3 genera and 4 species. These included *Stalolidia stali* Nielson, *Stalolidia crista*, n. sp., *Dicodia* n. sp., and *Docalidia meditabunda* (Spångberg).

ACKNOWLEDGMENTS

Material described in this paper was kindly furnished by Dr. Norman Penny, California Academy of Sciences, San Francisco, and formerly with the Instituto Nacional de Pesquisas da Amazonia (INPA); Dr. K. G. A. Hamilton, Agriculture Canada, Ottawa (CNC); Dr. Paul H. Freytag, University of Kentucky, Lexington (UKL); and Dr. Paul W. Oman, Oregon State University, Corvallis (OSU). To these colleagues I express my sincere gratitude. I thank Jeanette Price and Sun Young Kim for the excellent illustrations, and Dr. Oman for reviewing the manuscript and offering useful comments.

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HABITAT USE BY BREEDING MALE SAGE GROUSE: A MANAGEMENT APPROACH

Kevin L. Ellis[1,2], Jimmie R. Parrish[1], Joseph R. Murphy[3], and Gary H. Richins[4]

Abstract.—Radio telemetry was used to study habitat use of breeding male sage grouse (*Centrocercus urophasianus*) at a lek in northeastern Utah during 1983 and 1984. Objectives were to determine if grouse day-use areas differed significantly in sagebrush characteristics from adjacent nonuse areas and to establish a simplified method for use by land managers in identifying grouse use areas. We determined that male grouse used areas of greatest sagebrush height and cover. Our methods provide a means for land managers to identify habitat associated with a lek that is suitable for male sage grouse day use in the event sagebrush alteration is planned within 3 km of a lek.

The dependence of sage grouse (*Centrocercus urophasianus*) upon big sagebrush (*Artemisia tridentata*) for cover and food is well documented (Patterson 1952, Eng and Schladweiler 1972, Wallestad and Pyrah 1974, Wallestad and Schladweiler 1974). Modifications of sagebrush habitat used by sage grouse often lead to reduced bird numbers (Rogers 1964, Klebenow 1970, Martin 1970, Wallestad 1975), most likely because sage grouse are specific in their habitat requirements and cannot tolerate serious alterations of use areas (Patterson 1952). For these reasons, and because of the continuing decrease in sagebrush rangelands (i.e., 2.5 million ha between 1952 and 1977), sage grouse numbers continue to decline (Braun et al. 1977).

The objective of this study was to determine if areas used by breeding male sage grouse when not involved in lekking (i.e., day-use areas) differed significantly in sagebrush characteristics from adjacent unused sites.

Study Area

The lek studied was 8 km north of Duchesne, Duchesne County, Utah, at an elevation of 1,548 m (Ellis 1985). The terrain has little slope, and the region is dominated by big sagebrush and cactus (*Opuntia* spp.) interspersed with stands of mustard (*Brassica* spp.). Mean annual rainfall is 22.4 cm, and mean annual temperature is 6.8 C (range 0.6–37.8 C). The average frost-free period is 113 days. Oil production and winter livestock grazing are the major land uses of the region.

Methods

Roosting male sage grouse were captured on the lek at night 19 March–16 May 1983, and 21–24 March 1984, using techniques described by Giesen et al. (1982). Captured individuals were aged, measured (Beck et al. 1975), and fitted with radio transmitters (150–152 MHz) attached to either poncho collars (Amstrup 1980) or necklaces (Biotrack, Sautary, England). Telemetry equipment consisted of a mobile dual 4-element Yagi null-peak antenna system attached to a Telonics TR–2 receiver and a TDP–2 advanced digital data processor. Radio-tagged grouse were monitored 2–4 days per week and were typically located one to three times during the monitoring day between 2 April and 25 May 1983 and between 2 April and 17 May 1984. Tracking began 0.5–1.0 hr after grouse departed the lek and terminated 2 hr before sunset. Locations of birds were based on triangulation from three locations at distances 100–400 m apart. All angles were adjusted for previously determined bias (Springer 1979) and plotted on a 7.5-min. USGS topographical map. Each 2.56-km^2 section of the study area was divided into 36 equal cells (0.071 km^2/cell) (Fig. 1), and each radio location was classified into the cell that encompassed the majority of the error

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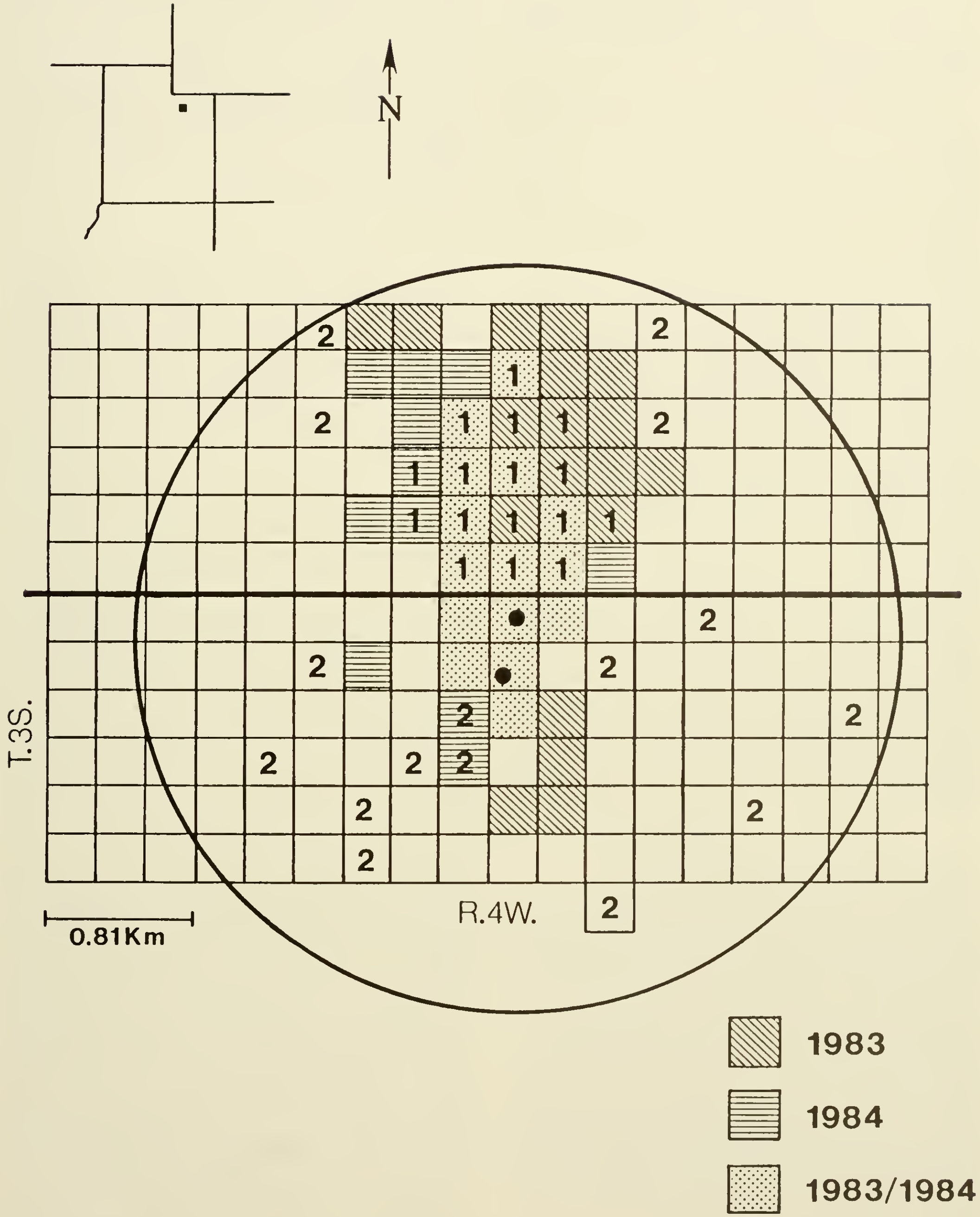
N
T.3S.
R.4W.
0.81Km
1
2
1983
1984
1983/1984

Fig. 1. Distribution of radio-tagged male sage grouse in relation to lek centers at an area in northeastern Utah. Lek centers are represented by black dots. 1 = location of use area vegetation transect. 2 = location of nonuse area vegetation transect.

polygon (Springer 1979) for that location. In addition, radio-tagged grouse were flushed at random intervals to visually determine whether individuals were associated with other males from the lek.

On this basis, grouse use was calculated for each cell and categorized as day-use or nonuse areas (Ellis et al. 1987). Sixteen point-center-quarter vegetation sites (Seber 1973) were selected within the day-use area, and 16 were selected at random in the nonuse area for analysis and comparison of sagebrush characteristics. Sites within the nonuse area were selected with the stipulation that each site could not be farther from the central area of the lek than the farthest radio location plotted during the study. Sagebrush cover (percent), height (cm), and density were measured along four transects extending 30.8 m in each of the cardinal compass directions from the center of each vegetation site (64 transects each in the use and nonuse areas). Only live sagebrush plants were measured along each transect. Percent cover was transformed for analysis using angular transformation (Sokal and Rohlf 1969). Sagebrush characteristics recorded along individual cardinal transects were pooled to provide an estimate for each vegetation site. Pooled estimates were tested for similarity using computer-generated, paired t-tests.

RESULTS AND DISCUSSION

Eight male sage grouse (7 adults, 1 juvenile) were monitored for 27 days between 2 April and 25 May 1983, and 10 adult males were monitored for 19 days between 31 March and 16 May 1984, yielding a total for both years of 252 radio locations. Dispersion flights from the lek to day-use areas were in a northeasterly direction and 0.5–0.8 km in distance (Fig. 1). The longest flight recorded was 2.1 km. Radio-tagged males were generally accompanied by 15–30 other males when flushed and were reluctant to fly on days with high winds or rain.

Sagebrush cover and height were significantly greater in day-use areas although sagebrush density was virtually identical in both day-use and nonuse areas (Table 1). Sagebrush cover in day-use areas ranged from 26.88 to 36.45% and from 8.58 to 36.15% in nonuse areas. Sagebrush height in day-use areas and nonuse areas ranged from 40.50 to 69.73 cm and 20.30 to 56.18 cm, respectively. Breeding male sage grouse appear to prefer day-use areas that have greater plant size than adjacent areas (Wallestad and Schladweiler 1974, Schoenberg 1982). On the basis of multivariate statistical analyses of sagebrush characteristics, Schoenberg (1982) concluded that sagebrush plant size was the most important habitat factor separating use from nonuse areas. Our results support the conclusion that breeding male sage grouse prefer day-use areas with sagebrush plants that are taller and greater in diameter than plants in adjacent areas.

TABLE 1. Characteristics (mean ± S.D.) of live sagebrush plants measured in 1983 and 1984 in sage grouse use areas of northeastern Utah, and t-test results of comparisons between use areas.

Area[1]	Cover[2]	Height[3]	Density[4]
Day-use	30.50 ± 2.88	53.20 ± 10.50	13.83 ± 2.32
Nonuse	25.99 ± 6.82	40.50 ± 10.80	13.56 ± 4.51

[1] N = 16.
[2] P = .02; t = 2.44, DF = 20.2.
[3] P = .002; t = 3.36, DF = 30.0.
[4] P = .84, t = 0.21, DF = 22.4

Alteration of sagebrush habitat in the vicinity of a lek may cause population declines or abandonment of an area by breeding sage grouse (Rogers 1964, Martin 1970, Wallestad 1975, Braun et al. 1977). In situations where sagebrush alteration or destruction is unavoidable within 3 km of a lek we suggest that the viability of that lek could be maintained if the land-use manager were able to either (1) protect the historical breeding male day-use areas and associated lek, or (2) in the event that these areas cannot be preserved, provide protection of adjacent areas with similar sagebrush stands within a 3-km radius of the lek. Recognizing that the land-use manager, in most cases, has neither the facilities nor the time to perform the complicated procedures (i.e., multivariate statistics) often used by researchers, we make the following recommendations to those considering sagebrush alteration in the vicinity of a lek:

1. When possible, protect all sagebrush within a 3-km radius of a lek as suggested by Braun et al. (1977).
2. If alteration is unavoidable within 3 km of a lek, identify day-use areas. This can be

accomplished by making 10–15 periodic visits to the lek, during the breeding season, and observing the departure of the strutting males. Once the day-use area has been located, make a walk-through inspection looking for signs of heavy grouse use in the area (i.e., droppings, dusting sites, feeding sites). This will allow a more specific definition of the use area. Once the core use area is identified, protect it and try to provide for a buffer around it if possible. Our data indicated that in both years the core day-use area was a minimum of 0.25 km^2 in size. Because grouse often walk to day-use areas, it is recommended that a continuous strip (i.e., travel lane) no less than 200 m be maintained between the lek and the designated day-use areas.

3. After day-use areas are identified and it is concluded that they cannot be protected, the manager should determine their basic physical sagebrush characteristics. Preservation of statistically similar adjacent stands along with an adjoining travel lane may provide male grouse with the necessary habitat to continue using the lek. Any planned alterations should be done after males have moved to summer or fall ranges.

ACKNOWLEDGMENTS

Financial support for this study was provided by Deseret Generation and Transmission Cooperative, Utah Division of Wildlife Resources, and the Department of Zoology at Brigham Young University. Appreciation is extended to C. M. White, B. J. Ellis, C. N. Ellis, M. Richins, N. Bingham, J. A. Roberson, and L. K. Swenson for assistance. The manuscript was improved by comments from T. D. Beck, E. D. Bailey, F. S. Guthery, and an anonymous reviewer.

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PHYSIOGRAPHIC CHARACTERISTICS OF PEREGRINE FALCON NESTING HABITAT ALONG THE COLORADO RIVER SYSTEM IN UTAH

Brandon L. Grebence[1,2] and Clayton M. White[1]

ABSTRACT.—Portions of the Colorado, Dolores, Green, and San Rafael rivers in Utah were surveyed for the breeding Peregrine Falcon (*Falco peregrinus anatum*) from 1986 to 1988. Eleven physical variables were measured at nest cliffs (N = 22) and nonnest cliffs (N = 22) to discern descriptors of cliff choice and subsequent occupancy by breeding peregrines in unexplored habitat within the Colorado River and its tributaries. Ratio scale measurements were subjected to discriminant function analysis or the Mann-Whitney test to determine significant differences between cliff types. At nest cliffs, Rayleigh's and Kuiper's tests were applied to compass directions to ascertain mean direction and circular uniformity. None of the variables we selected revealed any appreciable descriptive ability, which suggests that certain physical attributes of a nest cliff are of questionable value in forecasting occupancy by breeding peregrines within that particular habitat.

Historical breeding density of the Peregrine Falcon (*Falco peregrinus anatum*) west of the Rocky Mountains was perceived as "extremely low, and this surely is not due to lack of knowledge" (Bond 1946: 107). In the early 1970s an analysis of Utah revealed 40 historical or recent breeding sites, but the majority (80%) were located within the Great Basin. Five of the 8 locations (65%) within the Colorado Plateau were suspected but not verified (Porter and White 1973). The 1975 North American Peregrine Survey suggested the possibility of only 6 additional breeding sites along major drainages of the Colorado Plateau (Fyfe et al. 1976). A survey of Glen Canyon National Recreation Area (GCNRA) in 1983 located 2 additional sites on the lower end of Lake Powell (USFWS report 1983). One year later U.S. Park Service lands occurring within Utah were comprehensively surveyed, and peregrine breeding density within GCNRA was more completely described (Enderson 1984). In 1987 a follow-up survey of GCNRA revealed 5 previously unknown sites (Peregrine Fund Inc., unpublished report 1987). Six additional sites along the Colorado (2), Dolores (1), Green (2), and San Rafael (1) rivers were located during the 1986–1988 breeding seasons (Utah Division of Wildlife Resources, unpublished reports 1986, 1988).

Habitat evaluation near known breeding sites in Arizona revealed an apparent commonality of several traits and led to the formation of a predictive model for cliff occupancy by breeding adults (Ellis 1982). The habitat within Arizona, however, was very heterogeneous. A characterization of total peregrine breeding habitat in a more uniform habitat than Arizona has been attempted for the Colorado Plateau (Teresa 1989). Our study objective has been to identify within a more homogeneous habitat physiographic variables that reliably predict cliff choice and occupancy in previously unexplored habitat of the Colorado River and its tributaries.

STUDY AREA

The state of Utah is divided into four physiographic provinces: Basin and Range, Rocky Mountain, Colorado Plateau, and Basin and Range–Colorado Plateau Transition (Stokes 1977). The Colorado Plateau (eastern and southern one-third of Utah) has many subdivisions but, for the sake of simplicity, is further subdivided into two sections: the Uinta Basin and Canyonlands (Murphy 1981). The Canyonlands section comprises the southeastern quarter of Utah and is dissected by three major rivers: Colorado, Green, and San Juan. Only the San Juan River remains essentially unsurveyed for the presence of peregrines.

Between 14 and 17 June 1988 one of us (BLG) surveyed the Green River from the mouth of the San Rafael River to Mineral Bottom, and during 9–14 July 1987 from Mineral

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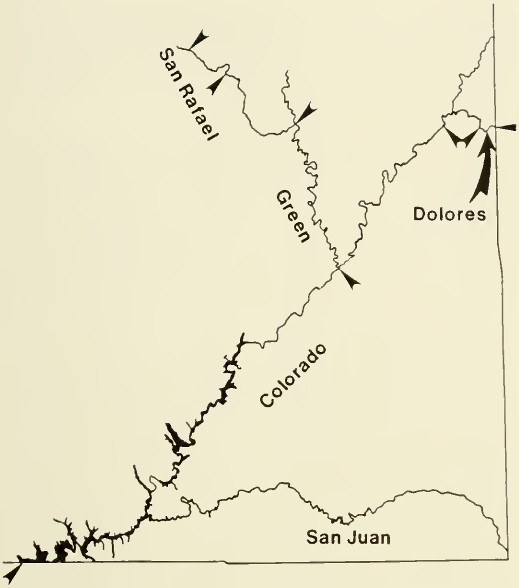

Fig. 1. River sections surveyed (denoted by arrows) on the Colorado, Green, Dolores, and San Rafael rivers for Peregrine Falcons in southeastern Utah.

Bottom to its confluence with the Colorado River (ca 163 km). One of the Green River's main tributaries, the San Rafael River, was surveyed from Buckhorn Wash to Swazy's Leap on 5–6 May 1988 (ca 49 km). Between 18 April and 16 June 1987 the Colorado River was surveyed from the eastern end of Professor Valley (ca 47 km east of Moab, Utah) to Page, Arizona (ca 462 km). The Dolores River (another Colorado River tributary) was surveyed from the Colorado border to the mouth of Fisher Creek on 22–23 April 1986 (ca 9 km; Fig. 1). Each of the aforementioned rivers probably contains nesting peregrines not observed in these surveys.

The majority of the Canyonlands section is classified as part of the Great Basin Desert (Larson 1970), with an annual precipitation of 13–20 cm (U.S. Dept. of Commerce NOAA-EDS 1973). Maximum and minimum recorded temperatures 1 April–30 June 1987 ranged from −3.3 C (1 April) to 40 C (14 June; NOAA Utah Climatological Data 1987).

Fremont cottonwood (*Populus fremontii*), the dominant tree along the Green, Dolores, and Colorado rivers, forms irregularly clustered communities in riparian zones. Thick vegetation typifies this riparian zone, primarily tamarisk (*Tamarix ramosissima*) interspersed with narrowleaf willow (*Salix exigua*), black willow (*S. gooddingii*), singleleaf ash (*Fraxinus anomala*), desert olive (*Forestiera pubescens*), Emory seepwillow (*Baccharis emoryi*), Rio Grande seepwillow (*B. salicina*), squawbush (*Rhus trilobata*), arrowweed (*Pulchea sericea*), and common reed (*Phragmites australis*). Floodplain regions along the Colorado and Green rivers have their own distinct community of shrubs, including four-wing saltbush (*Atriplex canescens*), torrey seepweed (*Suaeda torreyana*), greasewood (*Sarcobatus vermiculatus*), rubber rabbitbrush (*Chrysothamnus nauseosus*), viscid rabbitbrush (*C. viscidiflorus*), and skunkbush (*R. aromatica*). Vegetative communities above the cliff walls are dominated by blackbrush (*Coleogyne ramosissima*) and shadscale (*Atriplex confertifolia*). Tamarisk is ubiquitous in GCNRA where shoreline regions have sufficient soil to support vegetative cover. Rocky hillsides are dominated by xerophytic vegetation, predominantly blackbrush and shadscale (Flowers 1959). The diversity of plants promotes a diversity of prey species that may be a critical factor for peregrine numbers.

Persistent flooding of the Dolores River has prevented thick vegetative communities in its riparian areas. Talus slopes above the river and the communities above cliff walls are dominated by Utah juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus edulis*).

The dominant tree along the San Rafael River is also Fremont cottonwood, and the understory communities are predominantly tamarisk, greasewood, and four-wing saltbush. Talus slopes and areas above cliff walls are dominated by pinyon pine and Utah juniper (Foster 1968).

METHODS

A breeding site, or eyrie, is defined as a ledge or pothole in association with a nest scrape. A nest cliff is defined as the rock formation surrounding the eyrie (see Runde and Anderson 1986). Cliff brink is defined as that point where a rope is necessary for further downward travel. Cliff base is defined as that point of the talus slope where climbing skills are necessary for further upward travel.

Adult peregrines were initially located with a spotting scope or binoculars. Once a presumed breeding territory was located, a second visit was undertaken in order to confirm eyrie occupancy and location. Eyrie locations were plotted on USGS 7.5′ or 15′ topographic quadrangle maps by positioning a compass at an obvious land feature and recording azimuth to the eyrie. Eight of the nest cliffs were surveyed on land and the remaining 14 from a boat.

Actual eyrie location was determined by observing one adult relieve its mate from incubation. Once the exact eyrie location was ascertained, an azimuth (EYAZI) could be determined. A clinometer (Suunto PM–5/360 PC. Finland) was used to record percentage readings of the cliff brink, eyrie position, boundary between sandstone layers, and cliff base (Mosher et al. 1987, Runde and Anderson 1986). Each cliff section, together with its corresponding percentage reading, was multiplied by the cliff height (CHEIGHT: distance from the cliff brink to the cliff base) to yield estimates of eyrie height (EHEIGHT: distance from the cliff brink to the eyrie), eyrie to base height (EYBASE: distance from the eyrie to the cliff base), and sandstone layer height. Initially, a rangefinder was used in conjunction with the clinometer to determine CHEIGHT. When the calculated CHEIGHT was compared with the estimated CHEIGHT taken from a topographic map, a lack of consistency in rangefinder distances was evident. Apparently, excessive vibrations altered distance calibrations, which then produced erroneous measurements. Subsequently, estimated CHEIGHTs derived from topographic maps were used exclusively to determine EHEIGHT and EYBASE (Table 1).

In Britain, Ratcliffe (1962:25) observed, for peregrines and common raven (*Corvus corax*), that “in the most rugged country each species reaches a maximum breeding density and there is usually a large excess of suitable nesting cliffs.” The Canyonlands section of southern Utah contains some of the most rugged terrain in the United States (Murphy 1981). Accordingly, nonnest cliffs (N = 22) were selected arbitrarily along the same river corridors that had nest cliffs, the sole criterion being the presence of at least one obvious ledge or pothole that could function as an eyrie. Identical measurements were taken at nest and nonnest cliffs (Tables 1, 2). Nonnest cliffs were not selected at random because randomly selected sites could not always be included from a logistical standpoint. Furthermore, random selection could not always include cliff faces that contained ledges or potholes, which would render comparisons with nest cliffs meaningless.

A 5-km distance was used as a radius for each eyrie, based on the work of Enderson and Kirven (1983) and Mearns (1985), for the determination of total elevational gain (TOTGAIN), defined as the maximum elevation minus the minimum elevation found within that circle. Additional map measurements included the shortest distance to water (DWATER) and the corresponding azimuth (AWATER), cliff azimuth (CLAZI), cliff brink elevation (CELEV), and eyrie elevation (EELEV; Table 1). CHEIGHT estimation was determined from eyrie location–azimuth, which also provided CELEV. The cliff base reading on 15′ maps was determined from a land-area and slope-indicator template (Reproduction Specialties Inc.).

At nest cliffs, CLAZI, EYAZI, and AWATER were tested for significant mean directions by employing Rayleigh's test (Zar 1984), and for circular uniformity by using Kuiper's test (Mardia 1972). At both nest and nonnest cliffs, EHEIGHT, EYBASE, TOTGAIN, DWATER, and CELEV were subjected to a stepwise discriminant function analysis (DFA) using the SPSS statistical package (Nie et al. 1975) to determine differences between cliff types. CHEIGHT (the sum of EHEIGHT and EYBASE) and EELEV (equivalent to EHEIGHT) were determined to be confounding variables and were excluded from the analysis. The five variables entered into the DFA were well within the recommended sample size of at least three times the number of variables to be measured (Williams and Titus 1988).

Of the three sandstones of the Glen Canyon Group (Navajo-Kayenta-Wingate), the Kayenta Sandstone layer was utilized most frequently for eyrie placement (80%). An attribute of the Kayenta Sandstone layer is erosion into ledgy slopes (Baars 1972), which presumably provides a variety of nest sites from which to choose. Three variables of Kayenta Sandstone cliffs were compared for significant differences by using the Mann-Whitney test (Conover 1980; nest cliffs N = 12 and nonnest cliffs N = 11). These variables were Kayenta

TABLE 1. Characteristics of nest cliffs.

	Height (m)			Elevation (m)			Azimuth			
Site no.	Cliff[a]	Eyrie[b] to brink	Eyrie[c] to base	Cliff[d]	Eyrie[e]	Total[f] gain	Cliff[g]	Eyrie[h]	To water[j]	Distance to water[k] (m)
1	110	15	95	1341	1326	395	103	107	140	168
2	305	45	260	1524	1479	529	163	201	188	411
3	98	27	71	1780	1753	638	204	183	208	2478
4	122	19	103	1536	1517	418	131	90	134	518
5	79	5	74	1207	1202	444	108	125	124	74
6	274	17	257	1402	1385	303	14	55	48	257
7	183	54	129	1402	1348	340	214	217	223	183
8	98	28	70	1500	1472	566	110	68	90	808
9	122	45	77	1402	1357	354	60	51	48	91
10	140	45	95	1268	1223	517	97	25	112	152
11	134	28	106	1841	1813	595	170	153	135	2981
12	146	31	115	1487	1456	436	46	26	43	305
13	110	3	107	1329	1326	445	42	34	49	107
14	158	101	57	1621	1520	654	60	43	55	290
15	165	70	95	1292	1222	648	20	350	20	94
16	116	10	106	1640	1630	538	135	125	132	274
17	134	44	90	1353	1309	507	307	241	306	107
18	122	13	109	1402	1389	515	95	83	72	229
19	116	74	42	1244	1170	275	83	65	90	42
20	104	16	88	1232	1216	401	78	69	90	88
21	97	21	76	1865	1844	531	222	190	207	457
22	171	49	122	1609	1560	710	118	105	115	335
$\bar{x}$	141	35	107	1467	1433	489	101	90	103	475
SD	54	24	53	189	191	116	67	71	66	738

[a]CHEIGHT, [b]EHEIGHT; [c]EYBASE, [d]CELEV, [e]EELEV, [f]TOTGAIN, [g]CLAZI, [h]EYAZI, [j]AWATER, [k]DWATER (as referenced in text)

TABLE 2. Characteristics of nonnest cliffs.

	Height (m)			Elevation (m)			Azimuth			
Site no.	Cliff[a]	Eyrie[b] to brink	Eyrie[c] to base	Cliff[d]	Eyrie[e]	Total[f] gain	Cliff[g]	Eyrie[h]	To water[j]	Distance to water[k] (m)
23	146	35	111	1731	1696	829	293	246	307	442
24	61	11	50	1768	1757	638	62	32	204	3164
25	49	5	44	1585	1580	600	111	119	44	2012
26	61	6	55	1463	1457	611	135	107	115	351
27	146	6	140	1426	1420	390	64	63	64	76
28	110	14	96	1877	1863	594	205	158	222	640
29	122	9	113	1829	1820	589	203	181	157	1975
30	85	11	74	1853	1842	582	156	125	34	792
31	43	18	25	1323	1305	394	223	257	180	122
32	195	49	146	1780	1731	715	88	101	96	671
33	110	24	86	1451	1427	654	253	270	274	305
34	293	6	287	1634	1628	799	135	129	119	335
35	55	11	44	1183	1172	233	7	1	10	54
36	73	9	64	1280	1271	427	95	84	103	107
37	158	26	132	1560	1534	398	110	105	110	168
38	85	8	77	1244	1236	397	86	82	86	91
39	128	28	100	1256	1228	329	345	330	311	101
40	79	31	48	1207	1176	648	277	272	295	61
41	219	15	204	1499	1484	471	30	63	30	244
42	195	33	162	1402	1369	460	82	76	82	229
43	226	9	217	1353	1344	374	65	70	72	244
44	122	47	75	1402	1355	340	80	97	106	259
$\bar{x}$	126	19	107	1505	1486	521	97	94	85	566
SD	65	13	64	218	219	156	85	79	85	776

[a]CHEIGHT; [b]EHEIGHT; [c]EYBASE; [d]CELEV; [e]EELEV, [f]TOTGAIN, [g]CLAZI; [h]EYAZI; [j]AWATER, [k]DWATER (as referenced in text).

TABLE 3. Characteristics of Kayenta-Wingate Sandstone nest cliffs.

Site no.	Height (m) Cliff	Wingate	%	Kayenta	%	Eyrie (as a % of Kayenta)
3	98	62	63	36	37	75
4	122	90	74	32	26	60
5	79	47	60	32	40	18
8	98	70	71	28	29	100
9	122	77	63	45	37	100
11	134	106	79	28	21	100
12	146	90	62	56	38	56
13	110	107	98	3	2	100
16	116	97	83	19	17	50
17	134	90	67	44	33	100
18	122	83	68	39	32	33
21	97	67	69	30	31	70
$\bar{x}$	115	82	71	33	29	72
SD	18	17	10	13	10	28

TABLE 4. Characteristics of Kayenta-Wingate Sandstone nonnest cliffs.

Site no.	Height (m) Cliff	Wingate	%	Kayenta	%	Eyrie (as a % of Kayenta)
23	146	101	69	45	31	78
24	61	47	77	14	23	83
26	61	50	82	11	18	52
27	146	117	80	29	20	22
28	110	76	70	34	30	43
29	122	111	91	11	9	80
30	85	74	87	11	13	100
31	43	25	58	18	42	100
36	73	61	83	12	17	71
37	158	99	62	59	38	44
38	85	56	66	29	34	27
$\bar{x}$	99	74	75	25	25	64
SD	38	28	10	15	10	26

Sandstone height (KSH), EHEIGHT expressed as a percentage of the KSH, and the KSH expressed as a percentage of CHEIGHT (Tables 3, 4).

RESULTS

Traditional utilization of nest cliffs is a well-known aspect of peregrine breeding biology (Hickey 1942, Ferguson-Lees 1951, Cade 1960, Ratcliffe 1962, Newton 1976, White and Cade 1971, Mearns and Newton 1984). The persistence of the phenomenon has been hypothesized to involve prey specialization (Cade 1960), territorial familiarity and concomitant reproductive success (Newton 1979), the reduction of competition and stability of populations (White and Cade 1971), and insolation considerations (Cade 1960, Porter and White 1973, Kuyt 1980, Pruett-Jones et al. 1981). This habituation to specific nest cliffs was used to census and relocate 10 eyries discovered prior to 1986 (Enderson 1984).

Spacing regularity in unbroken habitat is an additional feature that describes peregrine breeding distribution (Beebe 1960, Cade 1960, Ratcliffe 1962, Newton 1976). A consistent minimum distance presumably is related to population stability (Ratcliffe 1962), the regulation of breeding density in accord with available resources (Newton et al. 1977), and the reduction of intraspecific conflicts during breeding or hunting (Newton 1979). Six additional eyries were discovered in 1986–1987 by assuming this regular spacing between eyries.

All four rivers contain sections characterized by a nearly continuous line of cliffs on either side, which face virtually every azimuth of the compass. Of the nest cliffs surveyed, 12 were Wingate and Kayenta sandstones and 3 were Navajo Sandstone. On lower Lake Powell, from Wahweap Marina to Mountain Sheep Canyon, 3 nest cliffs were Morrison Formation sandstones and 1 was Entrada Sandstone. Remaining nest cliffs ($N = 3$), located from Hite Marina to the mouth of the Green River, were Cedar Mesa Sandstone. Eleven of the nonnest cliffs were Wingate and Kayenta sandstones, 3 were Navajo Sandstone, 4 were Cedar Mesa Sandstone, and 4 were of sandstones of the Morrison Formation (Hintze 1973).

Univariate Analysis

Means and standard deviations of the three measured variables of Kayenta-Wingate sandstone cliffs are shown in Tables 3 and 4. No significant differences were revealed between nest cliffs and nonnest cliffs for the KSH ($p > .50$, Mann-Whitney), KSH expressed as a percentage of the CHEIGHT ($p > .15$, Mann-Whitney), and EHEIGHT expressed as a percentage of KSH ($p > .35$, Mann-Whitney).

For nest cliffs, CLAZI, EYAZI, and AWATER revealed significant mean directions (101°, 90°, and 103°; $p < .005$, $p < .01$, and $p < .005$, respectively; Rayleigh's test; Tables

TABLE 5. Classification results of discriminant analysis of physiographic characteristics of Peregrine Falcon nesting habitat along the Colorado River.

Actual group	N	Predicted group membership Nest	 Nonnest
nest	22	10 45.5%	12 54.5%
nonnest	22	5 22.7%	17 77.3%

[61.4% of grouped cases were correctly classified]

TABLE 6. Summary of stepwise discriminant analysis including the standardized canonical discriminant function coefficients for two of the five variables measured at nest cliffs and nonnest cliffs.

Variable	Step	Wilks' Lambda	Significance level	Standardized Discriminant Function Coefficients
EHEIGHT	1	.86	.01	.98
TOTGAIN	2	.84	.02	−.42

1, 2), and in each case azimuths were not uniform about the compass ($p < .05$, $p < .05$, and $p < .005$, respectively; Kuiper's test).

Discriminant Analysis and Classification

The key objective of the DFA is to predict group membership given a particular linear measurement (Williams 1983). The relative strength of this predictive ability is displayed on the classification table (Table 5). A cursory scan reveals the lack of a satisfactory separation between nest cliffs and nonnest cliffs. This effect may be the result of a violation of equality of the variance-covariance matrices, which distorts predictive ability, or the result of the arbitrary selection of nonnest cliffs. A test for the equality of two population correlation coefficients indicated that correlation coefficients of the two cliff types were equal. The implication of this result is a difference in variances. The variability in TOTGAIN and EHEIGHT is shown in Figure 2.

Two of the five variables, EHEIGHT and TOTGAIN, revealed significant group separation (Table 6). However, since the variance-covariance matrices were significantly different from each other ($p = .03$), a key assumption of discriminant analysis was violated. This may have compromised the ability of the DFA to effectively separate nest cliffs from nonnest cliffs.

DISCUSSION

While the relative importance of cliff height in determining breeding occupancy has been contested, Hickey (1942) maintained that, for the peregrine population east of the Rockies, extremely high cliffs represented an "ecological magnet" and were the single most important factor for occupancy. This concept was disputed as an "oversimplification when one tries to apply it in the west" (Bond 1946:107). Cade (1960) argued that the concept detracted from other factors that were better determinants. High cliffs were not considered requisite for nesting (Beebe 1960), nor were they preferred or related to nesting success (Herbert and Herbert 1965). Cliff height was discounted as unimportant for Colorado eyries, but total elevational gain was deemed to be significant (Enderson and Craig 1979). Ratcliffe (1962) countered that in Great Britain cliff height was an attractant and hypothesized that an increased choice of nest sites and security from intervention were responsible. He further suggested that total elevational gain as well as lateral extent were more important than the verticality of the nest cliff itself.

Figure 2 indicates that a wide range of topographical relief occurred at nest cliffs; it also shows that outlier cliffs had eyries positioned lower on the cliff face. This wide range reflects contrasts between the relationship of geological formations from location to location. TOTGAIN may be related to the stoop mode of hunting, where the peregrine "usually needs a considerable advantage in height over its intended prey" (Ratcliffe 1980:153). EHEIGHT has a rather narrow range with three exceptions (see Fig. 2). Again this effect is the result of geology. The majority (82%) of the nest cliffs had a sandstone layer (particularly Kayenta Sandstone), with numerous ledges less than 50 m from the brink of the cliff (Figs. 2, 3). It is possible that the arbitrary manner in which potential ledges were designated on noneyrie cliffs resulted in the weak separation of cliff types in the DFA.

Availability of a bathing site was considered requisite for cliff occupancy (Bond 1946, Cade 1960). Rivers were considered essential components of peregrine habitat in Alaska because they provided the erosional agent for formation of cliffs and they supplied the riparian habitat necessary for some of the preferred

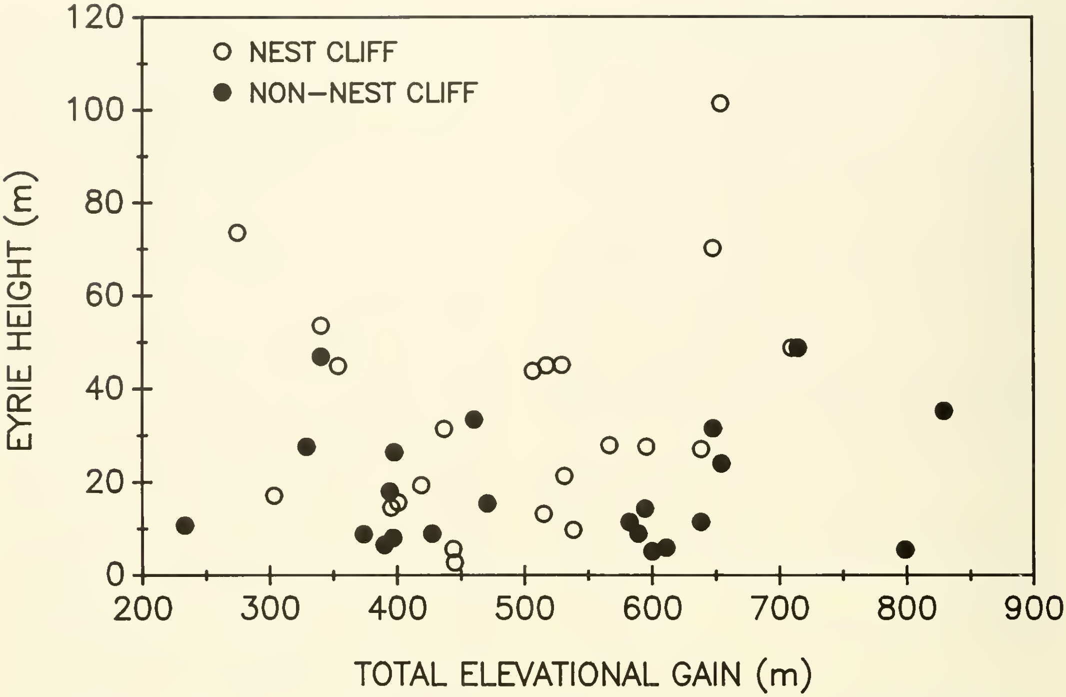

Fig. 2. Total elevational gain (TOTGAIN; X-axis) plotted against the distance from the cliff brink to the eyrie (EHEIGHT; Y-axis). The scales for both axes are in meters. Open circles represent nest cliffs, and closed circles represent nonnest cliffs. Those values separated from the main cluster of circles represent outliers.

prey (White and Cade 1971). Proximity to a perennial source of water was considered an attribute of most peregrine eyries (Porter and White 1973, Enderson and Craig 1979, Ellis 1984, White and Porter 1986), but the alleged property was not ubiquitous as suggested for Oregon (Gabrielson and Jewett 1940).

In our study, DWATER was biased in favor of nest cliffs that were confined to a river corridor, and the DFA suggests that this variable was not a significant predictor of cliff occupancy. Perhaps as additional nest cliffs within the Colorado Plateau are discovered, especially in side canyons of major river corridors, in Capitol Reef National Park, and in the San Rafael Reef, this variable will attain more predictive power.

In Alaska an avoidance of north-facing cliffs was noted by Cade (1960). He hypothesized that this was an adaptive response to summer storms that approached from the north. Canadian nest sites had a predominantly southern or western exposure, and it was suggested that early snowmelt freed those cliffs for breeding use (Kuyt 1980). Porter and White (1973) found that most eyries in Utah were on east- or north-facing cliffs (data were heavily weighted by the large proportion of eyries in the northern half of Utah). They suggested this represented a directional preference for the avoidance of insolation. In Australia most nest sites faced north or west, but directional variations were not significantly different from random (Pruett-Jones et al. 1981). However, when cliffs were grouped as north facing or south facing, a significant preference ($p < .01$) for north-facing cliffs emerged, and exposure was significantly related to fledging success ($p < .05$; Pruett-Jones et al. 1981). Climatic extremes were therefore postulated to cause the directional selection of the eyrie (Porter and White 1973, Pruett-Jones et al. 1981).

In Great Britain suitable nest cliffs faced all directions, and no directional preferences were detected (Ratcliffe 1962). Similarly, Colorado eyries revealed no consistent directional pattern other than an avoidance of the southern quadrant (135–225°; Enderson and Craig 1979). Ellis (1984) found that Arizona

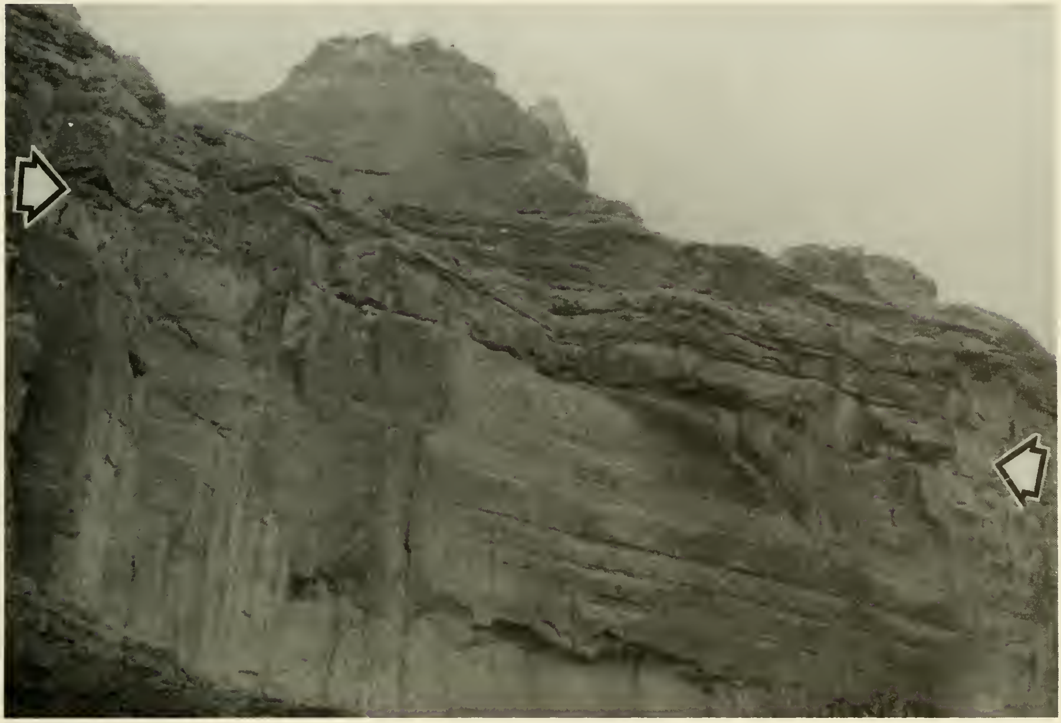

Fig. 3. View of cliff containing peregrine eyrie showing interface of Kayenta-Wingate Sandstone (arrow). The region of interface was also the region of eyrie placement.

nest cliffs faced predominantly north and west, with very few facing southward. However, when Ellis combined the Utah data (Porter and White 1973) with Arizona data, his resulting data indicated clearly that nest cliffs could face any direction. Ellis thus concluded that directional preference of cliffs could not be used as the sole criterion for occupancy even in a desert environment.

In our study nest cliffs had significant mean directions for both cliff and eyrie azimuths, and both were not uniformly distributed about the compass (Fig. 4). This implies a strong preference for the eastern quadrant (45–135°). However, our results are consistent with Ellis's contention that cliff orientation (and in this study eyrie orientation as well) cannot be used by itself as a predictor of occupancy.

Based on observations of Golden Eagle (*Aquila chrysaetos*) mortality, Nelson (1969) hypothesized that peregrines were particularly vulnerable to insolation extremes because of their habit of late seasonal nesting. Evidence of heat stress in both adult and nestling peregrines was noted at a south-facing eyrie in Alaska (Enderson et al. 1972). Golden Eagle eyries in Alaska and Utah revealed statistically significant directional preferences ($p = .01$), south-southeast in the arctic and north-northwest in the Utah desert. These results implied an avoidance of cold and heat, respectively (Mosher and White 1976). Ellis (1984) suggested that composition and arrangement of a peregrine eyrie, rather than directional orientation, were dictated by total insolation. Williams (1984) demonstrated the existence of an eyrie microclimate for the Prairie Falcon (*Falco mexicanus*) at an east-facing eyrie (95°) that presumably protected nestlings from ambient temperature extremes. Microclimate requirements should be progressively more exacting as the azimuth changed from east to south.

In our study 5 of 22 (23%) nest cliffs and their respective eyries were situated in the southern quadrant (Fig. 4). All 5 eyries were deeply recessed ledges, and 4 of 5 had a large rock on the brink of the eyrie, which provided additional shade (Fig. 5). The structure of

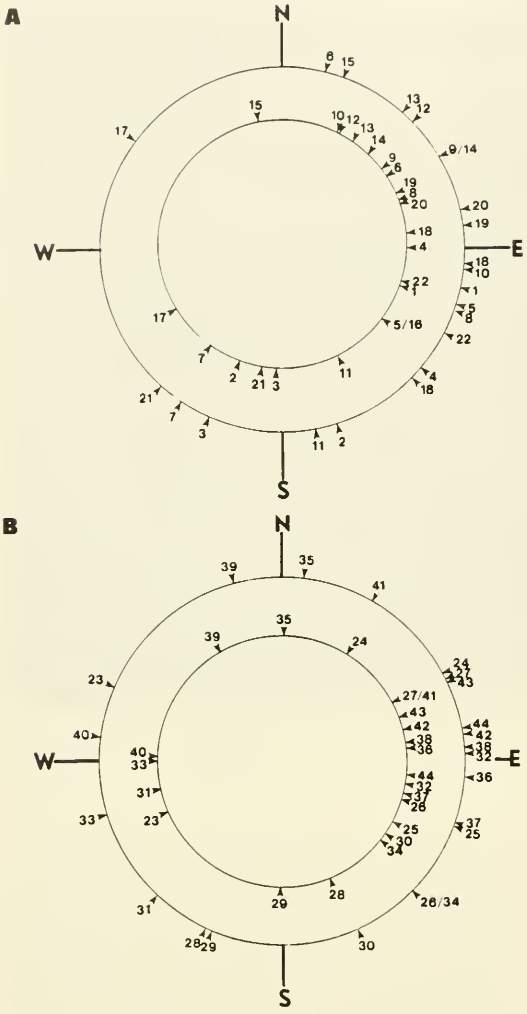

Fig. 4. Cliff and eyrie azimuths of nest cliffs (A) and nonnest cliffs (B) along the Colorado River and its tributaries 1986–88. Arrows on inner circles (N = 22) indicate eyrie azimuths, and arrows on outer circles indicate cliff azimuths (N = 22). Numerical values correspond to specific sites listed in Tables 1 and 2.

these south-facing eyries probably provided a microclimate that ameliorated total insolation and maintained a critical level of atmospheric humidity essential for successful hatching (Ratcliffe 1980), as 11 young fledged from these 5 sites (2.2 young/occupied site, unpublished data). These reproductive values compare favorably with normal fledging rates (Ratcliffe 1980). Fledging success at southern quadrant eyries in a desert environment implies that a similar microenvironment is realized within deeply recessed ledges such as those produced by northern and eastern cliff azimuths.

Additionally, desert environments frequently have considerable wind. This is especially true in canyons. We were unable to measure the effect of wind, but it may also ameliorate temperatures and allow some otherwise seemingly unsuitable cliffs to be used. Also, rain, especially when driven by prevailing winds, may influence the use of certain cliff facings or cliff and eyrie variables as shown in Australia (Olsen 1988). But, likewise, we gathered no data on this in our study.

Our results suggest that peregrines select eyries that ameliorate solar radiation in one of two ways: by selecting a cliff or eyrie with a northern or eastern azimuth, or by selecting an eyrie that nullifies insolation (e.g., deeply recessed ledges). The overall results of our study are in accord with the contention of Cade (1960:238) that "there is no very convincing evidence of so close a correlation between the physical characteristics of cliffs and the history of their occupancy by peregrines."

Finally, we conclude with three salient observations of the "red rock country" of the southern third of Utah: (1) Nest cliffs composed of all three sandstones of the Glen Canyon Group will usually have eyries situated in the Kayenta Sandstone. (2) Spacing regularity appears to be a useful attribute for locating additional nesting peregrines. So far, this spacing seems to be on the order of 6–14 km between sites. (3) Cliffs should not be excluded from a breeding survey because of a preconceived notion concerning azimuth.

ACKNOWLEDGMENTS

We thank D. A. Boyce, Jr., J. D. Brotherson, K. T. Harper, B. A. Maurer, and J. R. Parrish for helpful suggestions and critical review of earlier drafts of this manuscript. We are grateful to J. H. Enderson for the invitation to BLG to participate in the survey of Lake Powell and for his help in many ways. B. A. Maurer and W. H. Whaley assisted in data analysis. We also thank numerous personnel of the Park Service, the Bureau of Land Management, and the Utah Division of Wildlife Resources for technical and logistical assistance. Beatrice Grebence was a great

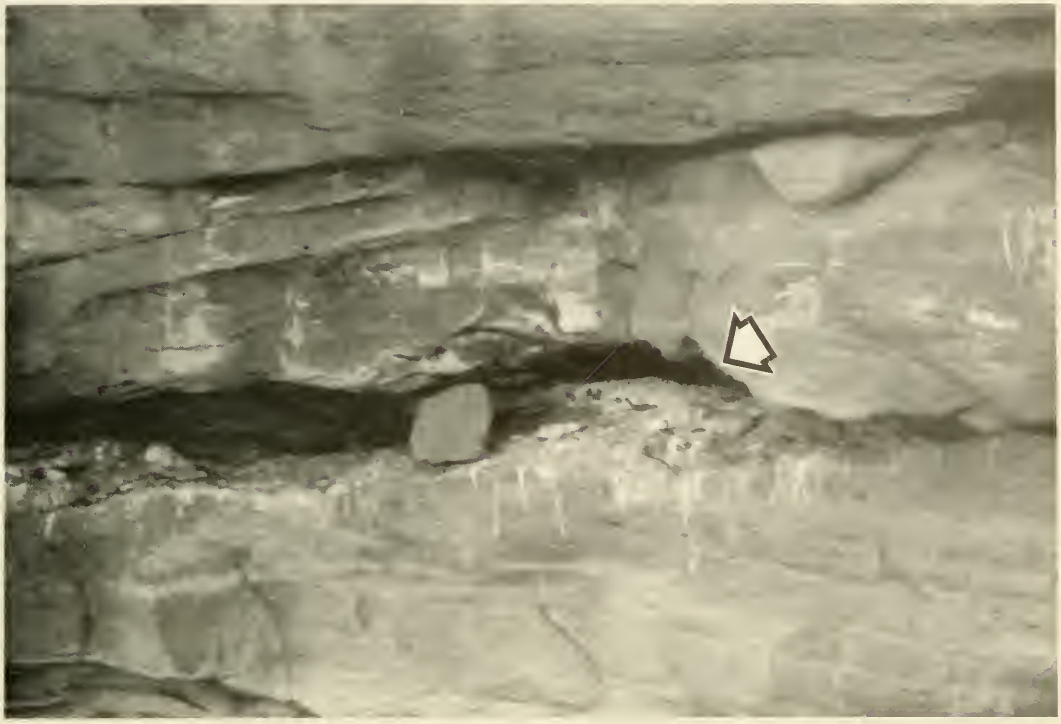

Fig. 5. Close up of a south-facing eyrie. Note the deep recess containing the eyrie (arrow) and large rock characteristic of eyrie ledges on south-facing cliffs.

help through all phases of the study. This work was supported by the Utah Division of Wildlife Resources and the Department of Zoology at Brigham Young University.

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SOIL-SITE RELATIONSHIPS OF WHITE LOCOWEED ON THE RAFT RIVER MOUNTAINS

Michael H. Ralphs[1], Brock Benson[2], and J. Cameron Loerch[2]

ABSTRACT.—White locoweed (*Oxytropis sericea* Nutt.) is restricted to the top and windswept ridges of the Raft River Mountains. Elevation and soil characteristics have the greatest effect on its occurrence. It is most abundant on the subalpine windswept ridge ecological site (9.2 plants/m^2) above 2,380 m. White locoweed apparently can tolerate the extreme environmental stresses of the shallow, rocky, windswept ridges where it is one of the dominant species. White locoweed also occurs in the deep, subalpine loam site (3.8 plants/m^2) above 2,865 m, but it is a minor component of this plant community. It is apparently less competitive on the deeper soils, and its population fluctuates more. It exhibits an opportunistic survival strategy on the subalpine loam site by having a large reserve of viable seeds in the soil ready to germinate and establish when environmental conditions are favorable, and then declines with competition from more robust species.

White locoweed (*Oxytropis sericea* Nutt.) is one of the most widely distributed locoweeds. It occurs on the plains, prairies, and foothills of the Rocky Mountains and is common from western Montana to the Black Hills of South Dakota, south to Oklahoma and central New Mexico, and occasionally westward to southern Utah, northeastern Nevada, and southern Idaho. It occurs mostly between 900 and 2,100 m altitude, occasionally reaching 3,350 m in the southern Rockies (Barneby 1952).

White locoweed is locally present on the top of the Raft River Mountains in northwestern Utah, where it has caused substantial livestock loss by inducing locoweed poisoning (James et al. 1981) and high mountain brisket disease (James et al. 1983). Historical reports (Gordon Carter, personal communication, 15 October 1983) indicate that white locoweed occurred lower on the sides of the mountains than it does presently. Currently, it is restricted to the flat mountain top. The objectives of this study were to describe the ecological sites and soils where white locoweed occurs and to define the relationship of white locoweed populations to soil characteristics and associated plant communities.

METHODS AND MATERIALS

An order 3 soil survey was conducted on mountainous rangelands of western Box Elder County in 1984 by the Soil Conservation Service (SCS) and the U.S. Forest Service. Ecological sites (synonymous with range sites in SCS terminology) were delineated and described. White locoweed occurred on four ecological sites near the top of the Raft River Mountains but did not appear on any other mountain ranges in the survey. The four sites differ in respect to elevations and soils. In 1985 a cluster of three paced transects was established in the center of each site where it occurred on the mountain. Twenty 0.1-m^2 plots were located along the transects at 10-step intervals. The number of mature and juvenile white locoweed plants in each plot was counted. Plants with three or fewer pinnately compounded leaflets were considered juvenile. Data were analyzed by analysis of variance (ANOVA) to compare differences among sites. Clusters within sites comprised the error term used in the F test. Where there were significant differences among sites, means were separated by Duncans multiple range test.

Percentage frequency of occurrence of white locoweed and other associated species was calculated to describe the plant communities on each site. Mean values for each cluster represented density or frequency of the species at each location. The mean of all clusters within an ecological site was calculated, and the standard error of the mean (SE) is reported to show the variability among locations within the same ecological site.

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Table 1. Soil families and ecological sites on which white locoweed occurs on the Raft River Mountains.

Soil	Symbol	Ecological site	Elevation (m)
Nielsen (loamy-skeletal, mixed, Argic Lithic Cryoborolls)	SAR	Subalpine windswept ridge	2,380–3,050
	LSR	Mountain windswept ridge (low sage)	< 2,380
Bickmore (loamy-skeletal, mixed, Argic Pachic Cryoborolls)	SAL	Subalpine loam	2,865–3,050
	HML	High mountain loam	2,600–3,050

Density, population dynamics, and production of white locoweed had been studied intensively at the Rosevere location since 1981. Seven permanently marked transects on the subalpine loam ecological site and five transects on the subalpine windswept ridge ecological site were read weekly from 1981 to 1986. Frequency of occurrence and the number of mature and juvenile white locoweed were recorded. The mean values averaged over weeks are presented for each year.

Weather records were obtained from the SCS snow survey and the Utah Climatological Bulletin to correlate changes in white locoweed density with weather patterns. Accumulation of winter precipitation as of 1 April was taken from a snow course station 4 km west at an elevation 100 m below the study site. Monthly precipitation during the growing season was obtained from the Snowville reporting station, 48 km east and 1,200 m below the study site. These weather records do not reflect the specific conditions at the study site but do indicate the trend of weather patterns for the region. Simple linear regression was used to compare the change in locoweed density over years and to determine the influence of precipitation on locoweed density.

Results

Description of Ecological Sites

Windswept ridge.—Soils of these sites are of the Nielsen family (loamy-skeletal, mixed Argic Lithic Cryoborolls), 25–50 cm to bedrock (Table 1). Coarse rock fragments comprise 35–65% of the volume. These sites occupy the shallow, rocky ridgetops and convex slopes. An elevational stratum occurs about 2,380 m (7,800 ft) in the plant community. Alpine sagebrush (*Artemisia scopulorum* Gray) is the dominant shrub on the subalpine windswept ridge site above 2,380 m, while low sagebrush (*Artemisia arbuscula* L.) dominates the mountain windswept ridge site below 2,380 m (Table 2). Bluebunch wheatgrass [*Agropyron spicatum* (Pursh) Scribn & Smith] and sandberg bluegrass (*Poa sandbergii* Vasey) are the dominant grasses on both sites. Fleabane daisy (*Erigeron leiomerus* Gray) and phlox (*Phlox hoodii* Rich.) are prevalent on both sites, but white locoweed is the dominant forb on the subalpine site. It occurs on the lower mountain site but at a much lower frequency (Table 2).

Loam site.—Soils of this site are of the Bickmore family (loamy-skeletal, mixed Argic Pachic Cryoborolls), 50–100 cm to bedrock. They are moderately deep and well drained and are limited to the flat mountain top and gentle, concave slopes. An elevational stratum of the plant community occurs about 2,865 m (9,400 ft), with subalpine big sagebrush (*Artemisia tridentata* ssp. *vaseyana* form *spiciformis* Osterh.) dominant in the subalpine loam site above 2,865 m and mountain big sagebrush [*Artemisia tridentata* ssp. *vaseyana* (Kydb.) Beetle] dominant in the high mountain loam site below 2,865 m. Kings Fescue [*Hesperochloa kingii* (Piper) Rydb.] is the most conspicuous grass in the subalpine site. Mutton grass [*Poa fendleriana* (Steud.) Vasey] is also abundant. Idaho fescue (*Festuca idahoensis* Elmer) and Kentucky bluegrass (*Poa pratensis* L.) are abundant grasses, and yarrow (*Achillia lanalosa* Nutt.) and orange sneezeweed (*Helenium hoopsii* Gray) are abundant forbs in both sites. Tailcup lupine (*Lupinus caudatus* Kellogg) is an important component at the high mountain loam site. White locoweed occurs at a relatively high frequency (22%, Table 2) on the subalpine loam site but is only rarely encountered in the high mountain loam site.

White Locoweed Density

Density of white locoweed was greatest on

Table 2. Percentage frequency of occurrence of species and standard errors of the means (±) on four ecological sites on the Raft River Mountains.

	Subalpine windswept ridge	Mountain windswept ridge	Subalpine loam	High mountain loam
White locoweed	50 ± 4	15 ± 1	22 ± 4	6 ± 3
Yarrow	22 ± 9	3 ± 2	65 ± 7	33 ± 7
Rose pussy toes	5 ± 2	13 ± 8	18 ± 2	10 ± 7
Buckwheat	2 ± 1	6 ± 6	18 ± 4	11 ± 4
Sneezeweed	0	0	18 ± 11	13 ± 4
Aster	0	1 ± 1	0	8 ± 4
Tailcup lupine	0	0	0	26 ± 7
Cinquefoil	6 ± 3	0	1 ± 1	
Fleabane daisy	28 ± 5	30 ± 10	2 ± 1	
Hoods phlox	24 ± 6	42 ± 10	6 ± 1	6 ± 3
Mountain big sagebrush	0	0	0	48 ± 8
Subalpine big sagebrush	1 ± 1	0	47 ± 6	0
Low sagebrush	0	46 ± 23	0	1 ± 1
Alpine sagebrush	20 ± 4	16 ± 6	0	0
Rabbitbrush	2 ± 1	1 ± 1	3 ± 2	4 ± 2
Idaho fescue	7 ± 9	0	35 ± 23	25 ± 9
Kentucky bluegrass	1 ± 1	0	26 ± 3	32 ± 6
Mutton grass	41 ± 3	13 ± 6	34 ± 9	16 ± 7
Sandberg bluegrass	65 ± 4	38 ± 4	24 ± 1	12 ± 5
Western wheatgrass	30 ± 6	10 ± 9	23 ± 10	22 ± 6
Kings fescue	2 ± 1	0	18 ± 1	9 ± 4
Junegrass	5 ± 2	16 ± 10	4 ± 2	3 ± 2
Bluebrush wheatgrass	26 ± 6	46 ± 24	3 ± 3	11 ± 4
Wheatgrass	0	0	1 ± 1	23 ± 10
Columbia needlegrass	0	0	0	6 ± 4
Elk sedge	2 ± 2	0	9 ± 2	7 ± 2

the subalpine windswept ridge site, with 9.2 plants/m^2 (Table 3). Density declined 47% on the same soil but below 2,380 m on the mountain windswept ridge site. Diverse topography prevented gradient sampling of white locoweed at descending elevations.

White locoweed is an important forb on the deeper Bickmore soils on the subalpine loam site above 2,865 m. However, its density is 60% less than on the subalpine windswept ridge site (Table 3). White locoweed plants on the subalpine windswept ridge site were smaller in size (leaflets 10–12 cm compared to 20 cm long) than on plants on the subalpine loam site. However, white locoweed contributed 38% to the total standing crop on the subalpine windswept ridge site compared to 12% of the standing crop on the subalpine loam site (Table 4).

There was a fairly strong line of demarcation in white locoweed density between the subalpine and high mountain loam sites. White locoweed overlapped slightly into the higher reaches of the high mountain loam site (0.8 plants/m^2), but it disappeared from the plant community below 2,740 m.

Table 3. Mean white locoweed density and percentage of plants that are juvenile and standard errors of the means (±) for four ecological sites on the Raft River Mountains.

Ecological site	Density (plants/m^2)	Juvenile (%)
Subalpine windswept ridge	9.2a[1] ± 0.63	27.6 ± 2.24
Mountain windswept ridge	4.3b ± 1.42	16.3 ± 6.35
Subalpine loam	3.8bc ± 0.87	20.2 ± 4.33
High mountain loam	0.7c ± 0.28	15.5 ± 7.81

[1] Means followed by the same letter are not significantly different as determined by Duncans multiple range test ($P < .05$).

The preferred habitat of white locoweed appears to be the shallow, subalpine windswept ridge ecological site along the top and ridges of the mountain (Fig. 1), but it is less dense on the subalpine loam and lower mountain windswept ridge sites. Elevation and soils appear to exert a strong influence on its density and restriction to the top of the Raft River Mountain.

Change in Density Over Years

Density on the subalpine windswept ridge

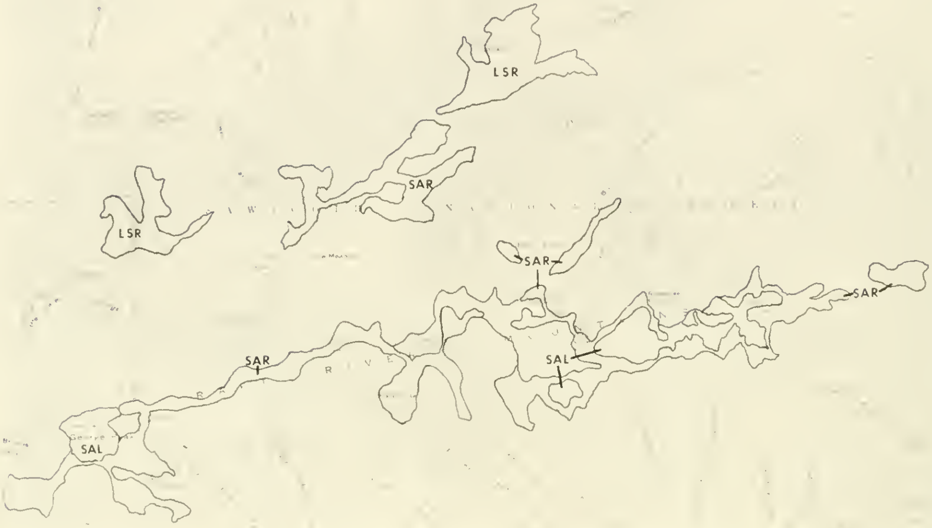

Fig. 1. Ecological sites on which white locoweed occurs on the Raft River Mountains. Subalpine windswept ridge = SAR, mountain windswept ridge (low sage) = LSR, and subalpine loam = SAL.

site in the Rosevere pasture remained fairly constant (Table 5). The slope of the regression did not differ significantly from 0. Density of white locoweed on the subalpine loam site declined linearly between 1981 and 1986 (r = −.93), and the slope of the regression differed significantly from 0 (P = .006).

There was low correlation (r = −.37) between winter moisture accumulation or growing season precipitation, and locoweed density on either site (Table 6). Total precipitation may be much different from effective precipitation due to wind movement and snowdrift accumulation. Most of the snow on the subalpine windswept ridge was probably blown off and accumulated elsewhere, creating a fairly constant, limited source of soil moisture. The snowdrifts on the subalpine loam site would be variable from year to year depending on the particular wind patterns.

DISCUSSION

The integrative effects of elevation, soil, and, perhaps, land form appear to restrict white locoweed to the top and windswept ridges of the Raft River Mountains. On the two windswept ridge ecological sites, white locoweed appears to have adapted a stress-tolerant survival strategy characterized by plants of arctic and alpine habitats (Grime 1977). The principal stresses are low temperatures, desiccating effects of strong winds, intense solar radiation, and mineral nutrient stress arising from low microbial activity in the soil (Grime 1977).

The extreme environmental stresses on the windswept ridge limit the presence of the more robust and competitive species (Grime 1977) such as mountain big sagebrush, Kentucky bluegrass, Kings fescue, and *Agropyron* species. White locoweed and other species on this site, while probably not more competitive than the robust species, are better able to withstand the environmental stresses. White locoweed on this site is much smaller, but more dense, than it is on the subalpine loam site, which is consistent with other observations of life forms of plants adapted to

TABLE 4. Standing crop (kg/ha) of forage classes and standard errors of the means (±) on high mountain subalpine loam and subalpine windswept ridge ecological sites in Rosevere pasture in 1985 on the Raft River Mountains.

Site	Grass	Forb	Sage	Loco	Total
Subalpine loam	465 ± 99	172 ± 24	0	89 ± 32	726
Subalpine windswept ridge	223 ± 37	62 ± 13	31 ± 15	147 ± 30	463

TABLE 5. Density of locoweed (plant/m^2) and standard errors of the means (±) on two ecological sites in Rosevere pasture on the Raft River Mountains. Probability of significant regression (P) between locoweed density and years, and correlation coefficient (r) are also given.

Year	Subalpine loam	Subalpine windswept ridge
1981	18.2 ± 1.55	13.1 ± 1.12
1982	11.2 ± 0.95	12.7 ± 1.09
1983	7.8 ± 0.67	9.9 ± 0.84
1984	6.4 ± 0.54	13.0 ± 1.11
1985	5.0 ± 0.43	10.3 ± 0.88
1986	3.4 ± 0.32	9.8 ± 0.91
P	0.006	0.13
r	−.93	−.67

nutrient-poor and stressful environments (Tilman 1985, Grime 1977). White locoweed is one of the first species to commence growth in the early spring; it remains green and succulent throughout the summer and is still green when covered by snow in the fall. It is also one of the more tolerant species to abnormal freezing temperatures during the growing season. On 5 and 6 July 1986, an abnormal cold front moved through the region. Temperatures at the nearest meteorological weather recording station at Grouse Creek (20 km west and 800 m below the study site) dipped below freezing on those two days. Temperatures at the study site must have been extremely low because most of the vegetation was frozen and turned a straw color. The flowers of white locoweed that were in bloom were frozen and aborted, but the leaves remained green and continued to grow.

The shallow, rocky habitat favored by white locoweed on the Raft River Mountains is similar to the coarse soils and dry habitat of white locoweeds described by Payne (1957) on the plains and foothills of the Rocky Mountains in Montana. The most important factor influencing its occurrence and density is the presence of coarse fragments in the soil. Payne (1957) speculated that the coarse fragments provide an interface for water percolation and accumulation. The long tap root could tap this deep, stored water and flourish in a harsh, xeric environment. The ability to tap deep-water storage in rocky soil, combined with tolerance of environmental stresses, may create a unique niche for white locoweed in the windswept ridge ecological site on the Raft River Mountains.

White locoweed is a minor species on the subalpine loam ecological site where it appears to exhibit a temporal or opportunistic survival strategy. Its density was extremely high in 1981 but declined during the remainder of the study. The decline did not appear to be related to precipitation. Other locoweed species exhibit large population fluctuations (Ogden et al. 1987). Population outbreaks may occur and dominate extensive areas for one or two years and then die off until the next time environmental conditions are favorable (James et al. 1968, Marsh et al. 1919, Ralphs and Bagley 1988). White locoweed is more stable than other locoweed species, but it does experience significant fluctuations in plant density (Marsh 1909).

TABLE 6. Winter and growing season precipitation recorded near the study site on the Raft River Mountains in northwestern Utah.

Season	Year 1981	 1982	 1983	 1984	 1985	 1986
			Precipitation (cm)			
Winter accumulation[a]	46	91	91	70	47	59
Growing season[b]	1.5	10	18	7	5	5

[a] Snow course located 4 km west of and 100 m lower than study site. Accumulation of precipitation as of April 1 each year.

[b] Cumulative monthly precipitation June–August collected at Snowville, 48 km east of and 1,200 m below study site.

White locoweed seed have hard, impermeable seed coats and remain viable and in great abundance in the soil for many years (Ralphs and Cronin 1987). Germination rate in the laboratory (Ralphs and Cronin 1987, Ziemkiewicz and Cronin 1981) and in field trials (Payne 1957) is very low. This may be an ecological advantage, since a large, dormant seed reserve is retained in the soil to permit exploitation of favorable environmental conditions (Harper 1967). The opportunistic germination and establishment cycle of white locoweed may allow it to successfully compete in nutrient-rich, deep, subalpine loam ecological sites under conditions of relaxed competition.

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ROLE OF POST-PLEISTOCENE DISPERSAL IN DETERMINING THE MODERN DISTRIBUTION OF ABERT'S SQUIRREL

Russell Davis[1] and David E. Brown[2]

ABSTRACT.—Abert's squirrel is a forest-dwelling mammal, dependent upon ponderosa pine, that now ranges from southern Wyoming to northern Mexico. During the late Pleistocene, ponderosa pine and this squirrel occurred no further north than central Arizona and New Mexico. In consequence, the present range of the squirrel north of the 36th parallel must have been the result of post-Pleistocene (Holocene) dispersal. If such dispersal took place after the fragmentation of the northern montane conifer forest, at least some leakage across barriers of unsuitable (non-ponderosa pine) habitat must have occurred. Dispersal following transplanting "experiments" has shown that such barriers can be crossed; other evidence is provided that suggests this may occur sufficiently often to produce significant changes in distribution within short periods of time. Thus, explanations for the distribution of Abert's squirrel, based only on historical legacy and local extinctions, are found to be insufficient. An alternative explanation is proposed in which post-Pleistocene dispersal also plays an important role.

The present distribution of the Abert's squirrel, *Sciurus aberti*, extends discontinuously from northern Mexico to southern Wyoming (Fig. 1). These disjunct populations have been thought to be Pleistocene relicts (McKee 1941). Presumably, during the late Pleistocene Abert's squirrel was widely distributed throughout a vast coniferous forest. With Holocene aridity, this forest, with its Abert's squirrel component, fragmented and retreated to higher elevations. Supposedly, since this arboreal squirrel is restricted to coniferous forests, dispersal across the resulting woodland gaps was impossible. In consequence, the squirrel was thought to be a helpless prisoner of geography (Goldman 1928, Turbak 1987a) and of a fragmented post-Pleistocene forest (McKee 1941); the distribution since the Pleistocene could only be influenced by local extinction.

However, a study of presence and absence showed a distributional pattern for Abert's squirrel that was consistent with one influenced strongly by dispersal (Fig. 2). In consequence, the traditional historical legacy explanation for the present distribution of Abert's squirrel now requires reexamination.

SQUIRREL DEPENDENCE ON PONDEROSA PINE

While individual Abert's squirrels are occasionally observed in pinyon pine (*Pinus edulis*) woodland, Douglas-fir (*Pseudotsuga menziesii*) and spruce-fir (*Picea-Abies*) habitats (Nash and Seaman 1977, Brown 1984, Hoffmeister 1986), numerous studies have shown that reproducing populations are restricted to forests dominated by ponderosa pine (*Pinus ponderosa*) (Rasmussen 1941, Keith 1965, Patton and Green 1970, Patton 1975, Rasmussen et al. 1975, Stephenson 1975, Pederson et al. 1976, Stephenson and Brown 1980, Hall 1981, Brown 1984, Pederson and Welch 1985). Dependence on a base of ponderosa pine is a characteristic trait of the species and occurs in each of the now geographically isolated populations (compare Figs. 1 and 3).

With the reasonable assumption (Wettstein and States 1986) that there have never been any unique populations of Abert's squirrel capable of reproduction and continued survival in the absence of ponderosa pine (and which later independently developed the ponderosa pine dependency now characteristic of the entire species), we can be confident that this squirrel has never ranged beyond the geographical limits of the distribution of ponderosa pine.

HISTORY OF THE DISTRIBUTION OF PONDEROSA PINE AND ABERT'S SQUIRREL IN THE SOUTHWESTERN UNITED STATES

Ponderosa pine has had a long and complex

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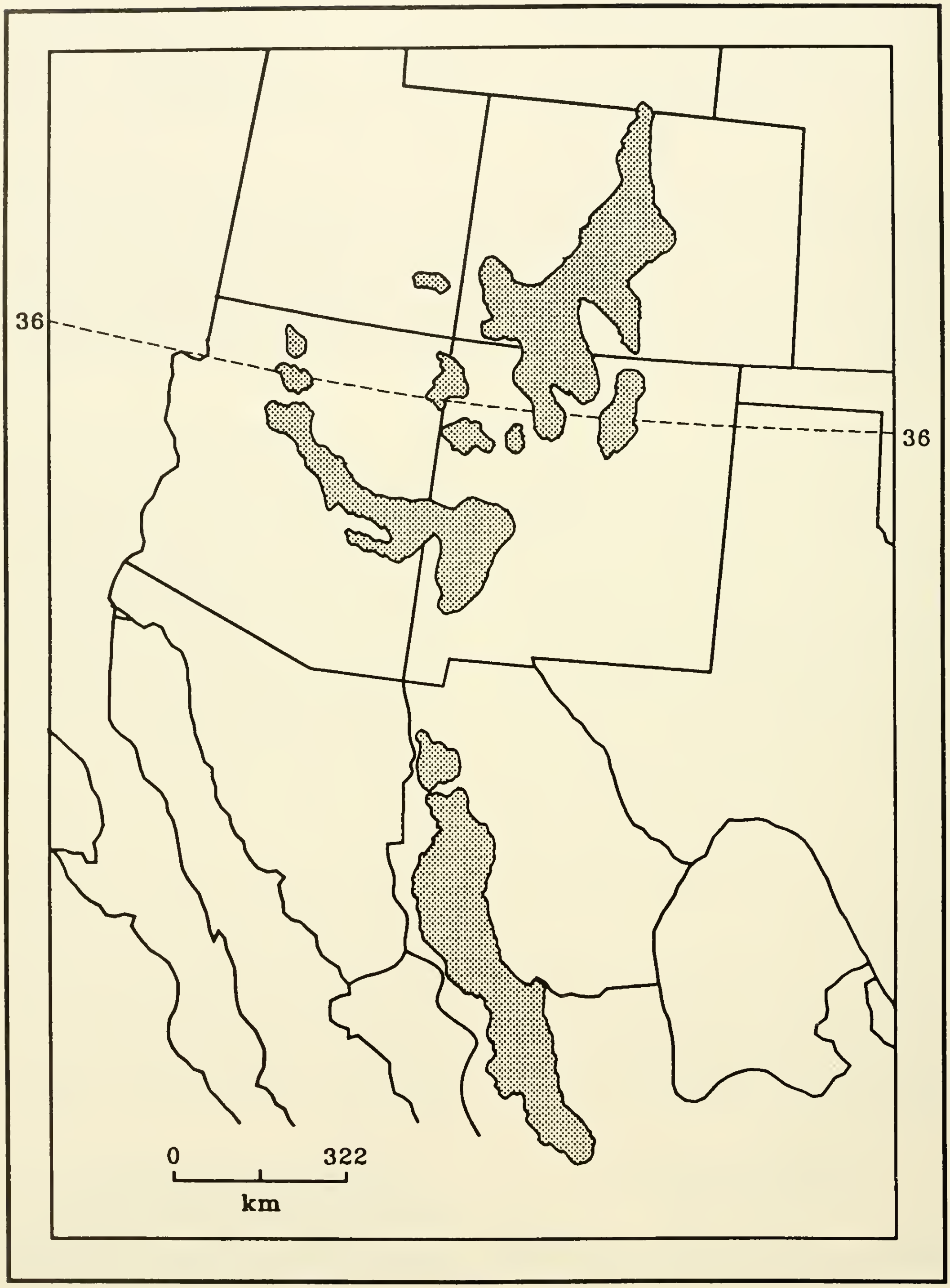

Fig. 1. The modern distribution of Abert's squirrel (modified from Hoffmeister and Diersing 1978, Brown 1984, and Davis and Bissell 1989). The dashed line for 36° North latitude designates the northern limit of ponderosa pine in late Pleistocene. Introductions are not included.

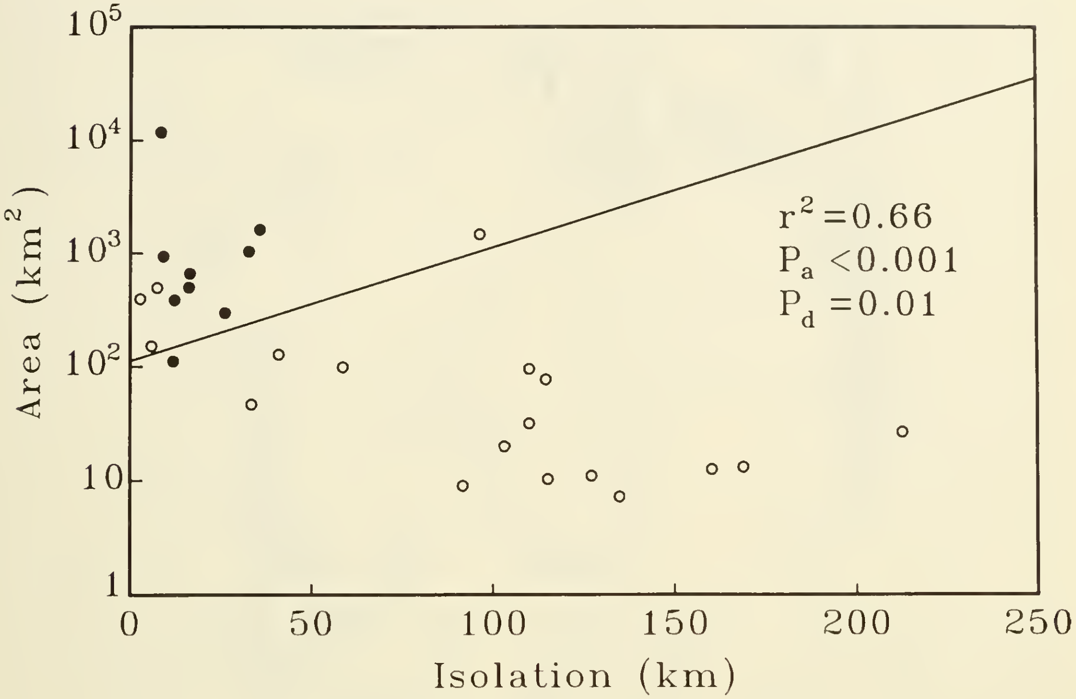

Fig. 2. Effects of area and isolation on the presence and absence of Abert's squirrel on 27 forest islands in the American Southwest (Lomolino et al. 1989; see also Lomolino 1986). Darkened circles indicate presence; open circles indicate absence. Probabilities that insular occurrence is not influenced by area (extinction) = P_a, and not influenced by distance (dispersal) = P_d.

history in western North America. Fossil plant parts similar to those of this species have been recorded from middle- and late-Miocene deposits in Nevada (Axelrod 1986). In the Pleistocene, these trees apparently occurred as far north as southern Wyoming during the Sangamonian interglacial (Baker 1986), but during the late Wisconsin glacial they were restricted in the United States to refugia in southern Arizona and New Mexico. During late Pleistocene, ponderosa pine is known no further north than 36 degrees North latitude (Betancourt and Van Devender 1981, Cole 1982, Thompson and Van Devender 1982, Wells 1983, Betancourt 1984, Spaulding 1984, Van Devender et al. 1987). In consequence, Abert's squirrel would not have been further north in late Pleistocene than north central Arizona and New Mexico (Fig. 1).

Beginning in early Holocene, climatic changes again favored dispersal of ponderosa pine northward beyond the 36th parallel into northern Arizona–New Mexico, and from there into Utah, Colorado, and Wyoming. Eventually, the vast northern conifer forest of the late Pleistocene (Lomolino et al. 1989) contracted into the isolated montane patches that exist today, now dominated at middle elevations by ponderosa pine. The rapid expansion of ponderosa pine into the huge, modern range it now occupies (Fig. 3) represents one of the most remarkable dispersal events of the Holocene (Van Devender et al. 1984).

The northward movement of ponderosa pine allowed a corresponding movement of Abert's squirrel. Populations of these squirrels now present in northern Arizona, New Mexico, Colorado, Utah, and Wyoming must have had their origin from populations that had previously been present in ponderosa pine forests south of the 36th parallel.

In northwestern Arizona, the squirrel somehow reached the north Kaibab (Fig. 1). Contrary to both traditional and popular opinion (Goldman 1928, Turbak 1987a, 1987b), the population now in the north Kaibab apparently

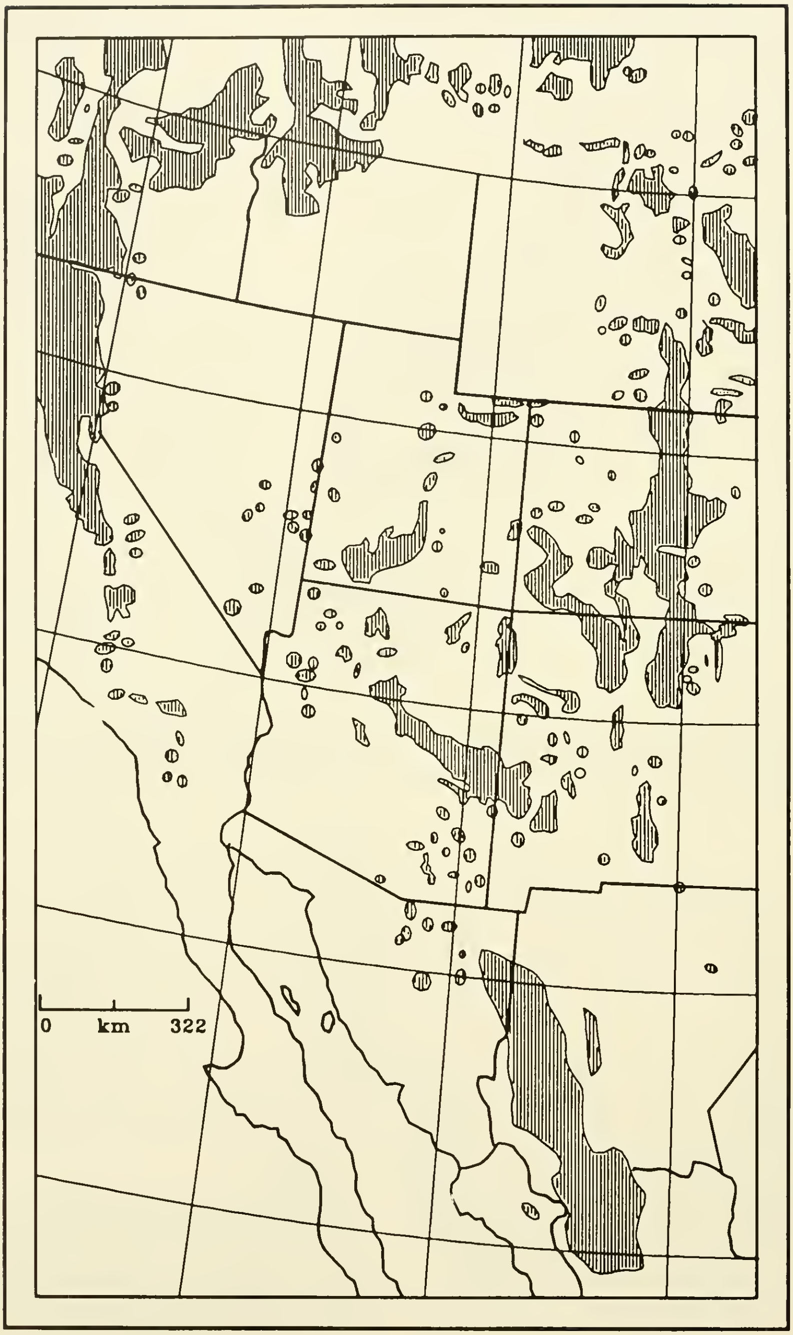

Fig. 3. Distribution of ponderosa pine in Mexico and a selected portion of the United States (Little 1971). While individual Abert's squirrels occasionally occur in habitats other than those dominated by ponderosa pine, at this scale any suggestion of the occurrence of populations of these squirrels (Fig. 1) outside the range of ponderosa pine is an artifact resulting from errors in the estimations of the distributions of one or the other of these two species.

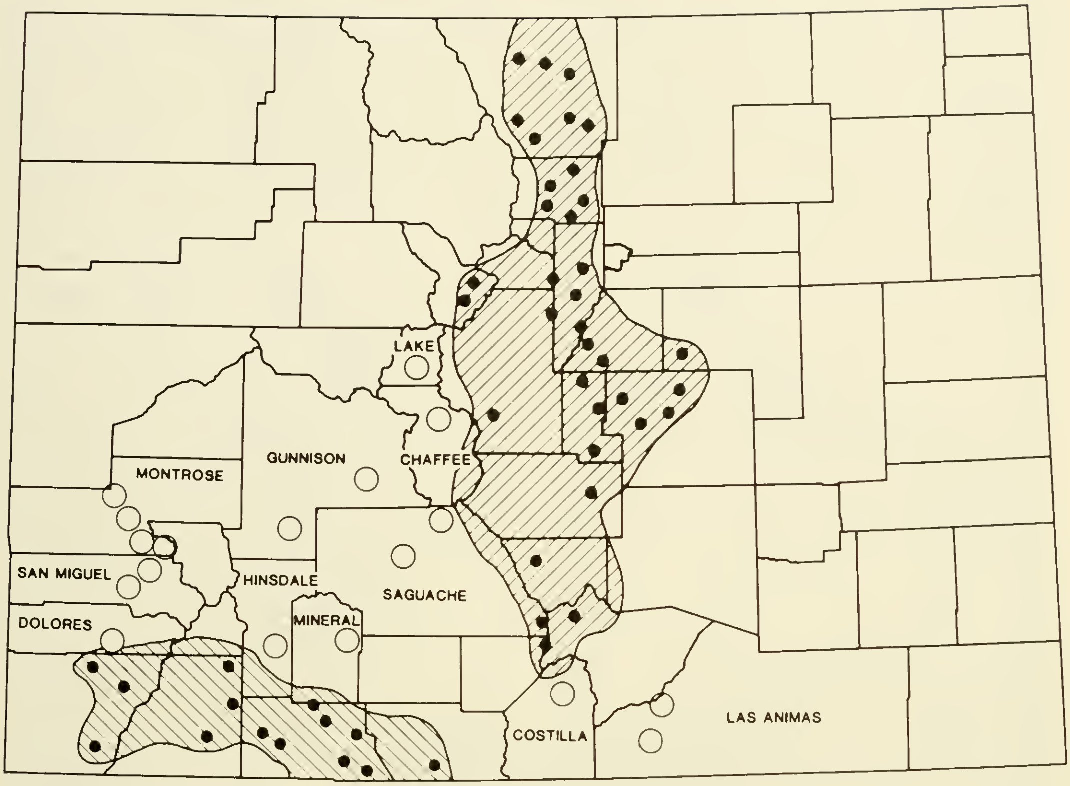

Fig. 4. Distribution of Abert's squirrel in Colorado (Davis and Bissell 1989). Cross-hatched area is Armstrong's estimate (1972), and black dots represent records he compiled. Localities indicated by open circles are the sites of post–1972 records; several sites close together are shown by a single open circle.

could not be a Pleistocene relict; there is no evidence of the existence of ponderosa pine forests north of the Colorado River until after the end of the Pleistocene.

In the absence of fossil evidence (Harris 1985), there is no way of knowing when the northward post-Pleistocene dispersal of Abert's squirrel began nor when the distribution of this species reached its modern extent. Forests dominated by ponderosa pine probably developed on the Colorado Plateau in the early or middle Holocene (Betancourt and Van Devender 1981), when the squirrel may or may not have been present. The chronology of certain records over the past 100 years, however, suggests that Abert's squirrel may not have reached parts of its present range north of the 36th parallel (Fig. 1) until quite recently.

For example, even though first recorded in southern Colorado in 1875 (Armstrong 1972), it was not reported in southeastern Utah until 1947 (Durrant 1952) nor in Wyoming until 1963 (Brown 1965). Based on observational records, a recent expansion of range has been reported in the southern and southwestern portions of Colorado (Fig. 4). Given its high visibility, it is unlikely that this squirrel could have escaped detection in all of these localities throughout historic time until its recent, fortuitous discovery. A hypothesis suggesting the relatively recent arrival of the squirrel in at least portions of its present northern range is certainly as well supported by available evidence as any to the contrary.

DISPERSAL ACROSS NON-PONDEROSA PINE HABITAT

Weighing against any hypothesis involving a role of post-Pleistocene dispersal is the present disjunct distribution of isolated montane patches of ponderosa pine forest in which this squirrel now occurs (Fig. 1; Lomolino et al. 1989). Northward post-Pleistocene dispersal by this squirrel beyond the 36th parallel could have taken place through continuous ponderosa pine habitat only if ponderosa pine arrived in the north prior to the disjunction of the massive late-Pleistocene forest. If dispersal occurred when vegetational conditions were similar to those existing today, then much of this must have taken place across apparent barriers of "unsuitable" (non-ponderosa pine) habitat. The presence of such apparent barriers is especially critical to our suggestion of the possibility of recent range expansion into Utah and into the southwestern portions of Colorado. The Abajo Mountains in southeastern Utah, the only Utah locality in which these squirrels occur, are separated by a gap of about 30 km of non-ponderosa–pine habitat from the nearest forests of southwestern Colorado (Lomolino et al. 1989). Likewise, the ponderosa pine forests in southwestern Colorado, north of the San Juan Mountains, are small and disjunct (Armstrong 1972) and comparably isolated. It is logical, then, to postulate that at least some gaps of non-ponderosa–pine habitat were likely to have been present whenever the northward, post-Pleistocene dispersal of Abert's squirrel occurred. To be plausible, a dispersal hypothesis such as this requires verification that these squirrels are capable of crossing such apparent barriers. Evidence for this comes from several sources.

First, even though reproducing populations of Abert's squirrel are restricted to ponderosa pine forests, Hoffmeister (1986) indicates that 20% of the locality records in Arizona are within pinyon-juniper woodlands. Consequently, there is no question that individuals can exist at least temporarily in pinyon-juniper habitat (Pederson et al. 1976) and should be capable of dispersal through this habitat at least for short distances from one ponderosa pine forest to another.

In addition, in central Arizona there is an example of a natural range expansion (not assisted by transplanting; Davis and Brown 1989) that must have occurred through intervening habitats of chaparral and woodland. In the Mazatzal Mountains there are a few small patches of ponderosa pine. These had been examined previously by personnel of the Arizona Game and Fish Department and visited by many hikers and hunters. Those who knew this mountain and its game mammals had been confident of the absence of these distinctive and obvious squirrels prior to the first record of their occurrence (in 1969 and 1970) in three of the forest patches (Brown 1984). About 10 years later their presence was reported about 32 km further south in this same range in another patch of ponderosa pine where there had been no previous sign of them. The ponderosa pine forest nearest to the Mazatzal Mountains is at least 50 km to the north.

Other evidence is provided from a reconstruction of the distribution of vegetation occurring in late Pleistocene (Lomolino et al. 1989). If this reconstruction is valid, then even in late Pleistocene the distribution of Abert's squirrel could not have been continuous and unfragmented. There apparently was never a continuous, late-Pleistocene connection between the extensive boreal conifer forest of central and northern Arizona–New Mexico and the austral conifer forest of northern Mexico. The closest approximation of such a connection occurred in southeastern Arizona where forests were present on montane islands surrounded by woodlands. These forests were only slightly less isolated then than they are today (Lomolino et al. 1989). Consequently, if dispersal through this region occurred at any time during the past 30,000 years, it could only have taken place because the squirrel was able to cross non-ponderosa–pine habitat barriers and island-hop from one montane island of ponderosa pine to another. It is interesting to note that while populations of this squirrel must have occurred on the mountains in southeastern Arizona at some time or another, these eventually became extinct. It occurs now only on a few of these mountains as the result of transplanting (Davis and Brown 1989). Such local extinction is not unexpected; these habitat islands are small.

Even stronger evidence for the ability of this squirrel to disperse through non-ponderosa–pine habitat was provided by biogeographical experiments resulting from a transplanting program conducted by the Arizona Game and Fish Department, beginning in 1940–41. Abert's squirrel was known to be absent from several isolated mountain ranges containing ponderosa pine, and it was thought

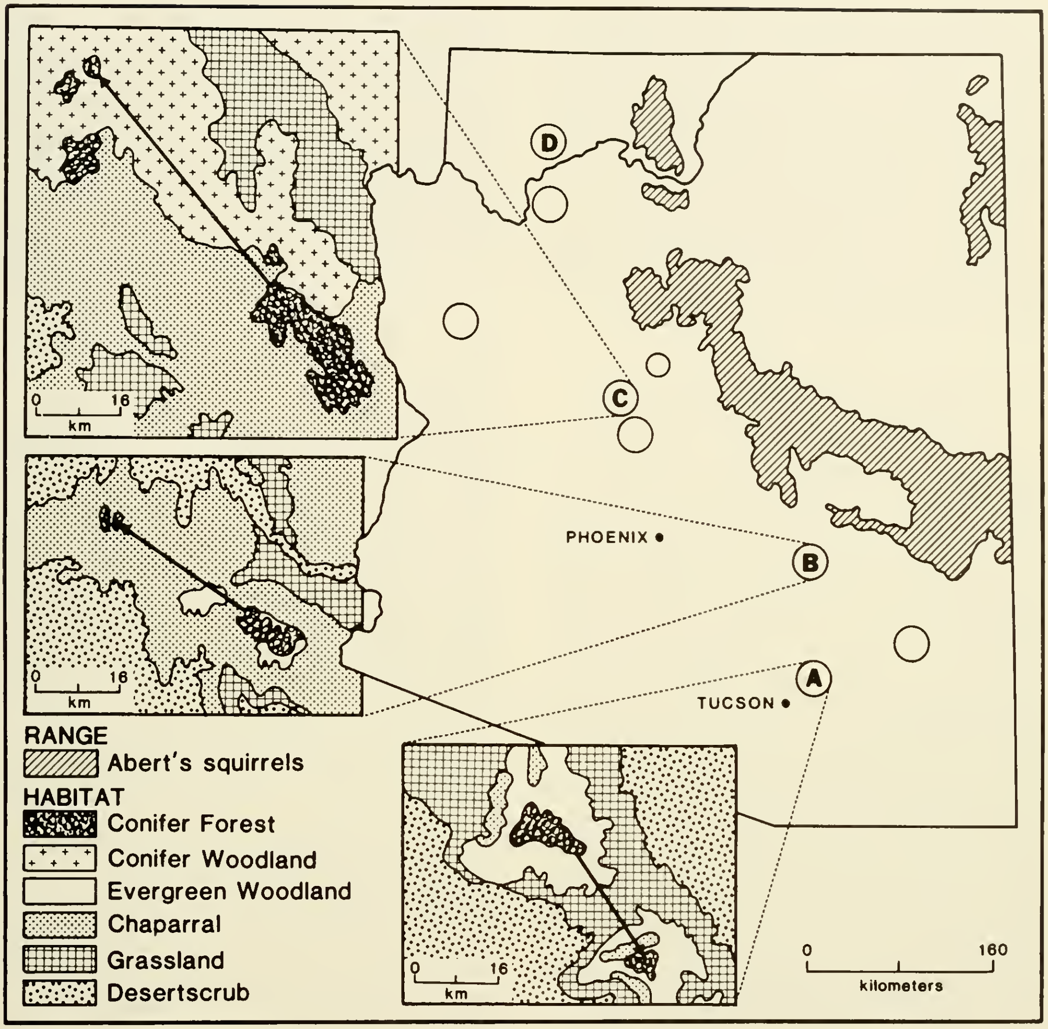

Fig. 5. The distribution of Abert's squirrel in Arizona (modified from Brown 1984), with examples of dispersal and colonization. Circles indicate sites of transplants (Davis and Brown 1989). A–D are transplants that were followed by colonization of nearby, isolated forests; and the straight lines with arrows for A–C are the shortest possible routes of dispersal; intervening habitats are indicated (from Brown and Lowe 1983). At D, the site of transplant was Mt. Logan, with subsequent dispersal through pinyon-juniper woodland to three nearby, isolated forests 8–12 km distant.

appropriate to transplant this squirrel into the larger of these. In several instances following release, the squirrel then dispersed through intervening nonforest habitats to colonize other smaller, adjacent forests from which it was also known to have been absent previously (Fig. 5). In these experiments, the time at which colonization was detected following transplanting increased with the distances between the isolated forests: 8 to 12 km in about 10 years (D in Fig. 5), 23 km in about 20 years (A), 29 km in 30 years (B), 57 km in 40 years (C). The intervening habitats include oak and pinyon-juniper woodlands, interior chaparral, and even semidesert grassland (Fig. 5). In each case, the sources of dispersing squirrels could have been from elsewhere than the sites of transplanting as indicated in Figure 5; if this were the case, however, the distances involved would then be even greater and the intervening habitats no less harsh (Fig. 5, and Brown and Lowe 1983). These are examples of natural dispersal and subsequent colonization; additional transplanting was not involved (Davis and Brown 1989).

Observations of individuals of any species dispersing through unsuitable habitat are rare. However, Cooper (1987) observed an Abert's squirrel crossing alpine tundra, 350 m elevation above treeline and at least 1,250 m above the ponderosa pine forest. Alpine tundra on mountain tops would seem to be even less suitable habitat for a tree squirrel than the woodlands at lower elevations in which individuals occasionally occur and through which much of the dispersal shown in Figure 5 must have taken place.

SUMMARY, CONCLUSION, AND DISCUSSION

Because all reproducing populations of *Sciurus aberti* are restricted to ponderosa pine forests, and since ponderosa pine is not known north of the 36th parallel in the late Pleistocene, two conclusions emerge: (1) this squirrel could not have been north of the 36th parallel prior to the arrival of ponderosa pine, and (2) post-Pleistocene dispersal must have played a major role in determining the modern distribution of the squirrel north of this latitude. While much of such dispersal may have occurred prior to the fragmentation of the vast northern forest of the late Pleistocene (but after the arrival of ponderosa pine), there remains the possibility that some dispersal of Abert's squirrel may have taken place considerably later when modern fragmented conditions existed. In fact, although unproven (and though alternate possibilities exist), there is evidence suggesting that this squirrel may have arrived rather recently in certain isolated portions of the northern part of its range.

In any case, once habitat conditions reached today's norms, no matter how much later dispersal may have occurred, at least some must have taken place across gaps in the distribution of ponderosa pine. Evidence from several sources clearly demonstrates that such gaps would not have prevented dispersal and that these squirrels are presently capable of colonizing isolated forests.

Historical legacy may have been involved in the distribution of this species south of the 36th parallel, and local extinction has apparently occurred at least on the montane islands in southeastern Arizona. All of the current range of this squirrel north of the 36th parallel, however, must have resulted from post-Pleistocene dispersal unimpeded by habitat barriers.

Abert's squirrel is absent from most of the ponderosa pine forests of North America (compare Figs. 1 and 3). In some cases this absence can be explained as the result of local extinction in small forests (as in the mountains of southeastern Arizona) or as a result of excessively low dispersal rates to the more isolated forests (Fig. 2). In addition, there is always the typical enigma of dispersal; some habitat and distance barriers are crossed while other barriers, apparently with higher probabilities of dispersal, are not (Fig. 2).

In any case, the lack of complete overlap of the distributions of these two species should come as no surprise. Abert's squirrel is dependent upon ponderosa pine, but the reverse relationship does not exist. These two species have very different characteristics. Abert's squirrels have poorer dispersal ability and a lower probability of successful colonization following dispersal. Also, reproducing populations of these mammals have much greater resource-area requirements.

In addition, their absence north of southern Wyoming suggests the possibility that these squirrels may be unable to exist in more northern climates and thus may have a narrower range of ecological tolerance. On the other hand, if the distribution of Abert's squirrel is as dynamic as we have proposed, and if they have reached both southern Wyoming and southeastern Utah only quite recently (as the chronology of records suggests), then we have no way yet of knowing what their potential may be for future expansion to either the north or west (compare Figs. 1 and 3).

This study involves only a single species of mammal, but the phenomenon demonstrated may have broad implications. If post-Pleistocene dispersal can so significantly influence the current distribution of *Sciurus aberti*, a species with an obligatory relationship with montane forests dominated by ponderosa pine, it could have a comparable influence on the distribution of other small, mountain-dwelling, nonflying mammals—especially those less restricted to montane habitats. The yellow-nosed cotton rat (*Sigmodon ochrognathus*) is such a species, and it has been shown to have recently expanded its range (Davis and Dunford 1987, Davis and Ward 1988). If this phenomenon should occur widely, then post-Pleistocene dispersal has played a major role in determining the modern patterns of distribution of montane forest mammals of the American Southwest. Analyses of both community- and species-level patterns and evidence that many forest-dwelling species occasionally occur in woodlands and other low-elevation habitats have provided strong support for this hypothesis (Davis et al. 1988, Lomolino et al. 1989).

ACKNOWLEDGMENTS

Several people reviewed preliminary versions of this paper and provided helpful suggestions: D. Armstrong, J. Betancourt, E. L. Cockrum, S. Cross, M. Lomolino, J. Mead, B. Patterson, R. Sheehy, R. Sidner, and T. Van Devender. C. Dunford and P. S. Martin helped with a major revision that eventually resulted in the present version. Discussions with J. Betancourt, J. Mead, and T. Van Devender, regarding ponderosa pine distribution during the late Pleistocene, were invaluable. Figures 1–3 were prepared by J. Abbott; Figures 4 and 5 were prepared by C. Ernstein.

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INFLUENCE OF EXPERIMENTAL HABITAT MANIPULATIONS ON A DESERT RODENT POPULATION IN SOUTHERN UTAH

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ABSTRACT.—This paper addresses how habitat manipulations in a black sagebrush (*Artemisia nova*)-dominated area, John's Valley of southern Utah, affected resident desert rodent populations. Rodents studied included the deer mouse (*Peromyscus maniculatus*), Great Basin pocket mouse (*Perognathus parvus*), sagebrush vole (*Lagurus curtatus*), Ord's kangaroo rat (*Dipodomys ordii*), and least chipmunk (*Eutamias minimus*). The experimental design involved analyses of treatment and control (nontreatment) plots rather than pre- and posttreatment of all plots. Habitat manipulations emphasized cutting of shrubs (rotobeating), treatment of plants with a herbicide (2,4-D), and reseeding with a mixture of grasses, forbs, and shrubs. Posttreatment trapping indicated the deer mouse was the most abundant rodent in treatment and control plots. Data indicate the prescribed habitat treatments had no significant negative affects on the deer mouse demes on the control or treatment plots. Habitat treatments may have negatively impacted recruitment in pocket mice. Least chipmunks were not captured in plots treated by rotobeating. Our habitat manipulations may have contributed to interspecific competition in this rodent community through the reduction of both food and cover.

Many ecological factors influence the dynamics of a cold desert rodent population. When aspects of the vegetational habitat are altered for management purposes, subsequent responses can be expected in rodent populations that reflect changes in interspecific relationships as well as changes in density, home range, reproduction, dispersal, recruitment, body size, and food habits. It is difficult to relate measured responses to specific changes of components in the habitat. Reason suggests an interrelated hierarchy of limiting factors operating either individually, in an additive fashion, or synergistically to elicit a series of responses from the impacted rodent population.

Previous studies of critical factors suggest that

> population density is a consequence of survival, reproduction, and dispersal of individuals. These processes are affected by the capacity to tolerate expressions of the physical environment, the availability of essential resources and interactions with other individuals of the same and different species (Brown and Munger 1985).

They have shown that limited food resources as well as interspecific competition within a guild of ecologically similar species play a major role in regulating the density of desert rodent populations.

Other studies have indicated that habitat manipulations adversely affect rodent food supplies and essential microhabitat (Taylor 1963, Weckey 1963, Holbrook 1979). Alternative conclusions resulting from Parmenter and MacMahon's (1983) habitat manipulations within a shrub steppe ecosystem suggest that shrub architecture and other shrub-related resources are unimportant to some rodents (e.g., deer mouse, *Peromyscus maniculatus;* Great Basin pocket mouse, *Perognathus parvus;* and northern grasshopper mouse, *Onychomys leucogaster*). Others have shown that the vertical and horizontal complexity of foliage do not correlate well with functional diversity of small mammals (MacMahon 1976, Grenat and Serranos 1982).

Johnson and Hansen (1969) found that 2,4-D (2,4-dichlorophenoxy acetic acid) herbicide treatments did not eliminate cover provided by stems and branches of shrubs killed by the treatment. They observed no significant differences in deer mouse density between treated and untreated rangelands.

The opportunity to further explore the relationships between small rodents and disturbances in their habitats came as a companion study of habitat alterations designed to benefit the Utah prairie dog (*Cynomys parvidens*), a threatened species (U.S. Fish and Wildlife Service, 49CFR2330). This suite of habitat-disturbing treatments, along with control

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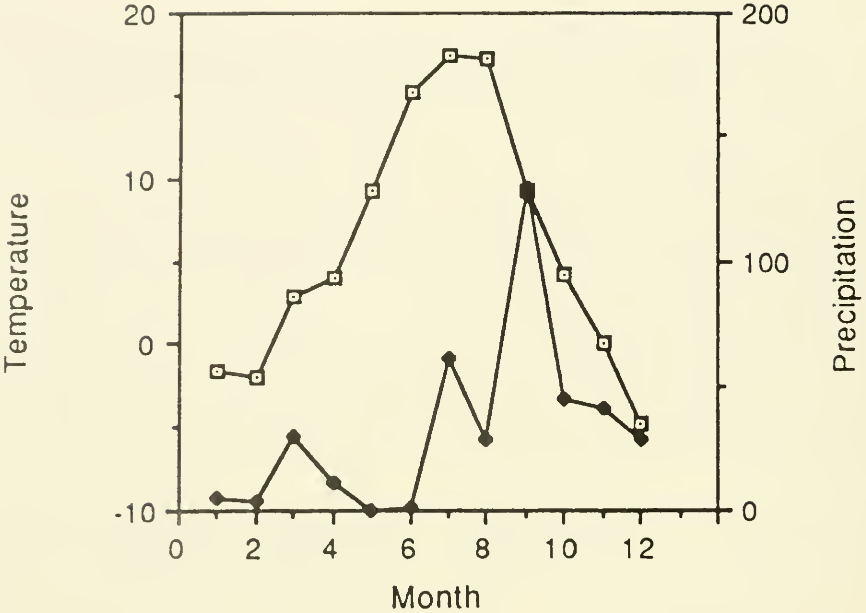

Fig. 1. Climatic diagram representing weather variables (temperature, C; precipitation, mm) measured at Bryce Canyon, Utah, during 1986.

areas, allowed examination and testing of the following hypotheses relating to small mammals (excluding *C. parvidens*):

1. Population densities of small rodents on treated plots would be reduced by a combination of factors including depressed reproduction, increased dispersal, and increased mortality.
2. The size of home ranges of the various rodent species would generally increase on treated areas.
3. Body weights of rodents, as an indicator of body condition, would be proportionately less on treated plots.
4. Diversity of rodent species would decrease in relationship to vegetational treatments; interspecific dominance by one or more species may be evidenced.
5. The effects of vegetational treatments can be quantitatively measured and expressed in ways meaningful to resident rodent populations.

STUDY AREA AND METHODS

The study site (2.56 square km) is just west of Widtsoe Junction, Garfield County, near Bryce Canyon National Park. It was established on lands administered by the state of Utah in what is known as John's Valley. The average elevation at the study site is 2,290 m, and, although the terrain is relatively flat, the northeast corner is dissected by a dry watercourse. Vegetation is primarily upper elevational cold desert shrubland. Dispersion of vegetation varies from open grassy areas to stands of closely or widely spaced shrubs. Dominant shrubs in this area are black sagebrush (*Artemisia nova*), fringed sagebrush (*Artemisia frigida*), carpet phlox (*Phlox hoodii*), dwarf rabbitbrush (*Chrysothamnus depressus*), rubber rabbitbrush (*Chrysothamnus nauseosus*), winterfat (*Ceratoides lanata*), and broom snakeweed (*Gutierrezia sarothrae*). Dominant grasses are western wheatgrass (*Agropyron smithii*) and squirreltail (*Elymus elymoides*). Prominent forbs are pretty rockcress (*Arabis pulchra*), vernal daisy (*Erigeron pumilus*), and longleaf phlox (*Phlox longifolia*). Scientific names of plants are after Welsh et al.(1987). Average monthly precipitation was 39 mm in 1986 but is highly variable (0 to 130 mm) from month to month. The wettest months of the year are from July to September. Mean monthly temperatures range from −2 C in January to 17 C in July (Fig. 1).

Studies were conducted on 12 plots, each 165 × 165 m and located at least 0.16 km from adjacent plots. The experimental design represented a randomized complete block with three replications. Three treatments

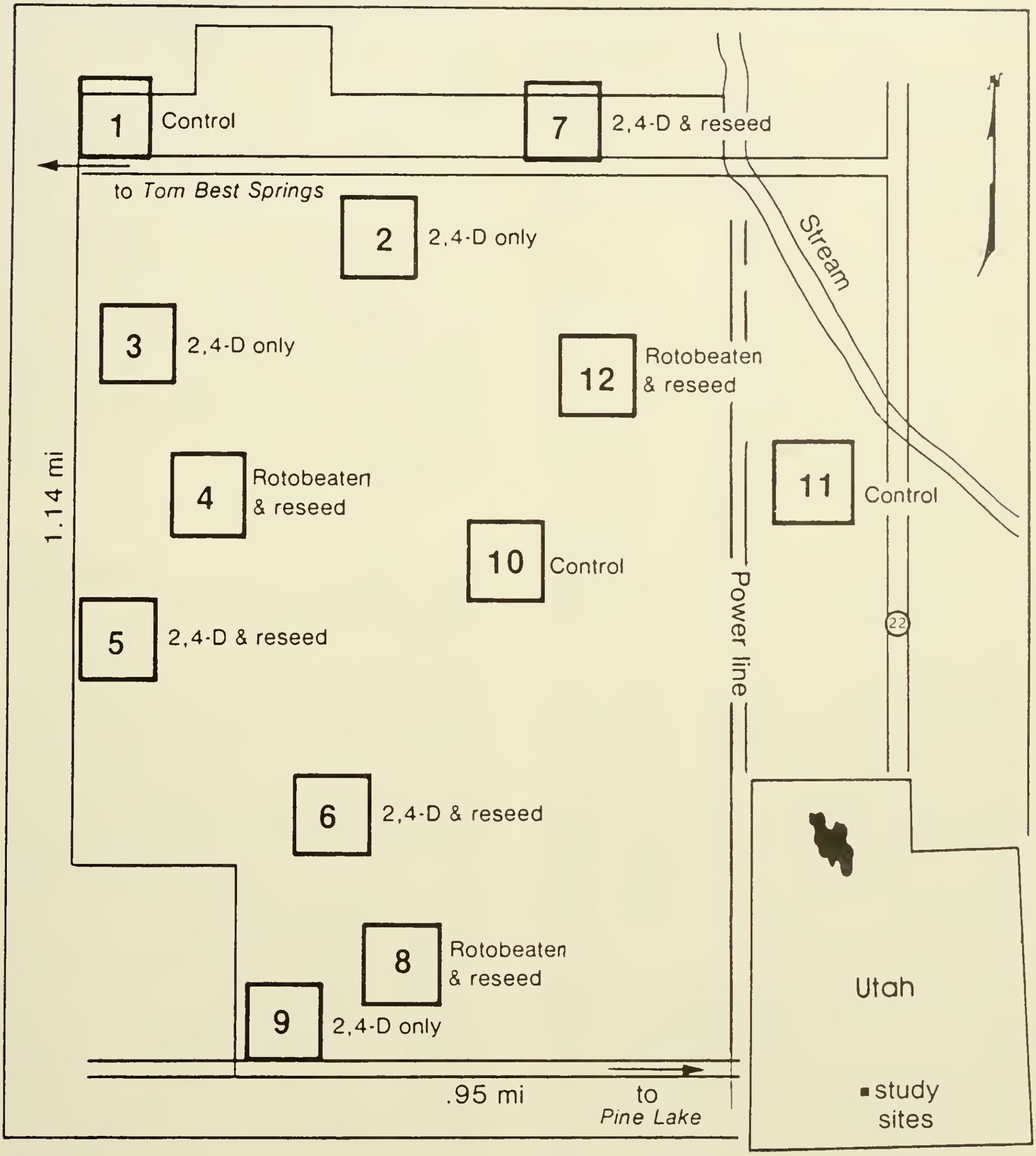
1 Control
7 2,4-D & reseed
to Tom Best Springs
2 2,4-D only
3 2,4-D only
12 Rotobeaten & reseed
Stream
N
4 Rotobeaten & reseed
11 Control
10 Control
1.14 mi
5 2,4-D & reseed
Power line
22
6 2,4-D & reseed
Utah
8 Rotobeaten & reseed
9 2,4-D only
.95 mi
to Pine Lake
■ study sites

Fig. 2. The location of the study site in southern Utah and the spatial relationship of the treatment and control plots.

(September and October 1985) included (1) mechanical shredding (rotobeating) followed by reseeding; (2) spraying with 3.3 kg/ha 2,4-D (2,4-dichlorophenoxy acetic acid) per plot; and (3) spraying with 3.3 kg/ha 2,4-D per plot followed by reseeding (Fig. 2). The 12 study plots were divided into three blocks with three treatment plots and one control plot in each block. All treated plots were enclosed with electrical wire fencing in May 1986 to prevent grazing by livestock.

Each plot contained a 10 × 10 station trapping grid with each trap 10 m apart; thus, 100 live-capture traps (38 × 11 × 11 cm) were monitored in every plot each day of trapping. Trap stations were permanently marked with a numbered stake. Traps were set on each plot for five consecutive nights during three trapping periods (5–23 May, 23 June–11 July, 4–22 August 1986). Traps were baited with a grain mixture after 6 p.m. and checked before 9 a.m. the next morning. This time interval allowed capture of diurnal as well as nocturnal rodents. Trapped mammals were identified and checked for sex, age (adult or juvenile), weight, reproductive condition, and station number where trapped. They were then marked by toe-clipping before their release. Trap nights were shifted slightly in August to avoid the rodent mortality expected when trapping during wet weather.

Density and projected canopy cover of shrubs on the treatment and control plots were measured by the point-quarter method (Mueller-Dombois and Ellenburg 1974). Vegetation biomass in each plot was estimated using a double sampling technique (Tadmor et al. 1975). Vegetation sampling occurred within a series of 30 randomly selected 1-m^2 quadrats (10 each on random lines) in each plot. There were three periods of vegetation sampling from May to September: (1) May–July, (2) July–early August, (3) late August–September. Vegetation was sampled concurrently with trapping. The difference between biomass of shrubs, forbs, and grasses (and grasslike plants) among treatment and control plots was tested using two-way ANOVA (Ott 1984). Similarity of vegetative composition in each plot was analyzed using a method based on the frequencies of observed plant species (Sneath and Sokal 1973). Regression analyses were used to investigate the relationship between diversity of vegetation and diversity of rodents (MacArthur 1972).

Population density of desert rodents was estimated from mark recapture data using Hayne's (1949) modified ratio method. This method assumes no individual mortality, emigration, immigration, or trap avoidance by the rodents under study during the trapping periods. Seasonal changes are expected in population densities of desert rodents; therefore, separate estimates were generated in each trapping period. The averages of the three estimates of population density in each treatment and control plot were used as summary data.

Those data derived from trapping rodents that did not follow a normal distribution were analyzed using nonparametric statistical methods to evaluate difference among treatment and control plots. The Kruskal Wallis test was used for paired comparisons within each trapping period (Siegel 1956).

Population dynamics of the deer mouse, pocket mouse, and other rodents were investigated between May and August 1986. Home range size of the deer mouse was estimated using the minimum area method (Dalke 1942, Mohr 1947, Stickel 1954). Only those animals captured three or more times with no more than two captures on the edge of the grids were included in calculations of home range. Data on size of home ranges were quantitatively transformed (Woolf 1968) to stabilize the variance among samples from treatments and control plots. A two-way ANOVA was applied to these data as a test for differences in home range size between deer mice among treatment and control plots during the trapping periods.

RESULTS

A total of 18,000 trap nights yielded 459 unique rodents for a trap success of 6.0%. Five species of rodents were caught; these included the deer mouse (*Peromyscus maniculatus*), 76.5%; Great Basin pocket mouse (*Perognathus parvus*), 13.7%; sagebrush vole (*Lagurus curtatus*), 2.6%; Ord's kangaroo rat (*Dipodomys ordii*), 1.3%; and the diurnal least chipmunk (*Eutamias minimus*), 5.8%. Deer mice are widely distributed and were caught on all plots. Minimal data were generated on the pocket mouse and other rodent species; thus, statistical analyses, to associate the effects of habitat manipulation on population characteristics, were confined to the deer mouse. The other species noted above were more restricted in distribution and were not present on all plots either because of overall low levels of population density or perhaps as a result of specific treatments. For example, least chipmunks were not captured on the rotobeaten plots. Estimates of population density were derived for each trapping period during the seasons of sampling (Table 1, Fig. 3).

For the deer mouse population, nonparametric statistical analysis suggested no significant difference among treatments and control plots within each trapping season (Table 2). The deer mouse increased on plots from May to August. Population increases were also observed for other rodent species, but the number of pocket mice did not change significantly among the three trapping periods (Fig. 4). In

TABLE 1. Estimates of mean population density (number per hectare $\bar{x}$ ± SD) of five rodent species in relationship to habitat treatment and control plots in southern Utah.

Species	Treatment[1]	Trapping period May–July	 July–Aug.	 Aug.–Sept.	Average number for three periods
Peromyscus maniculatus	1	3.4 ± 1.4	8.7 ± 1.3	21.5 ± 16.1	11.1 ± 11.4
	2	4.2 ± 4.8	5.4 ± 5.2	10.7 ± 3.5	6.8 ± 5.0
	3	1.7 ± 1.5	10.2 ± 7.1	17.7 ± 4.0	9.9 ± 8.2
	4	4.7 ± 1.7	10.0 ± 3.3	17.5 ± 7.8	10.8 ± 7.0
Perognathus parvus	1	2.0 ± 2.0	1.9 ± 1.9	2.6 ± 1.9	2.2 ± 1.7
	2	2.3 ± 2.2	2.5 ± 0.5	0.6 ± 1.0	1.8 ± 1.6
	3	0.3 ± 0.6	0.7 ± 0.6	0.0 ± 0.0	0.3 ± 0.5
	4	0.7 ± 1.2	1.6 ± 2.8	1.3 ± 2.3	1.2 ± 2.0
Eutamias minimus	1	0.3 ± 0.6	0.0 ± 0.0	1.2 ± 2.1	0.5 ± 1.2
	2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	3	0.7 ± 1.2	2.7 ± 4.7	0.0 ± 0.0	1.3 ± 2.9
	4	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 1.7	0.3 ± 1.0
Lagurus curtatus	1	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.2	0.3 ± 0.7
	2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	4	0.3 ± 0.6	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.3
Dipodomys ordii	1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	2	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.6	0.1 ± 0.3
	3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Total	1	5.7 ± 3.8	10.6 ± 2.7	26.0 ± 21.1	14.1 ± 14.2
	2	6.5 ± 2.8	7.9 ± 5.7	11.6 ± 4.0	8.7 ± 4.4
	3	2.7 ± 2.4	10.1 ± 11.7	17.7 ± 4.0	10.2 ± 9.0
	4	5.7 ± 3.1	11.7 ± 4.5	19.9 ± 9.6	12.4 ± 8.3

[1] Plot designations: 1 = control, 2 = rotobeating and reseeding, 3 = herbicide treatment, and 4 = herbicide treatment and reseeding.

TABLE 2. Comparisons of mean population densities of the deer mouse, using nonparametric analyses, on field plots during three sampling periods in southern Utah.

Composed treatments[1]	Kruskal-Wallis test May 5–23, 1986 P	 June 23–July 12, 1986 P	 Aug. 4–23, 1986 P
1,2,3,4	0.4465	0.7273	0.4593
3,4 vs. 1	0.8973	0.7963	0.7963
3,4 vs. 2	0.7963	0.3017	0.1213
1 vs. 2	0.7273	0.5127	0.2752

Plot designations: 1 = control, 2 = rotobeating and reseeding, 3 = herbicide treatment, and 4 = herbicide treatment and reseeding.

the first trapping period 16 pocket mice were caught, 20 in the second, and 14 in the third. Only 28% of the female pocket mice were pregnant, while fully 42% of the female deer mice showed this condition. For juvenile pocket mice, 50% were found on the control plots, 10% on the rotobeaten and reseeded plots, and 5% on the herbicide-treated plots. Thus, the habitat treatments may have had some negative effects on reproduction of pocket mice and perhaps survival of juveniles.

Female deer mice (because of pregnancies, 42%) had significantly higher average adult body weights than males [female 20.6 ± 3.7(g), male 19.0 ± 3.0(g), $F = 9.10$, d.f. $= 78.8$, $p < .05$]. There were no significant differences in body weights of deer mice among the treatment and control plots. (male: $F = 0.80$, d.f. $= 28$, $p > .05$; female: $F = 0.44$, d.f. $= 2.7$, $p > .05$).

Some dispersal of rodents between study plots was observed. In July one adult male deer mouse emigrated at least 300 m between plots. In addition, an adult male pocket mouse emigrated 157 m between plots. Trapping in August showed that three subadult deer mice (two males, one female) and one adult male pocket mouse had moved to plots different from those on which they were originally captured. Data compiled by this study cannot resolve whether these movements were normal, induced by habitat treatments, or related to species interactions predisposed by the August increase in the number of deer mice.

The size of home ranges established by the deer mouse was measured on different treatment and control plots. The average home

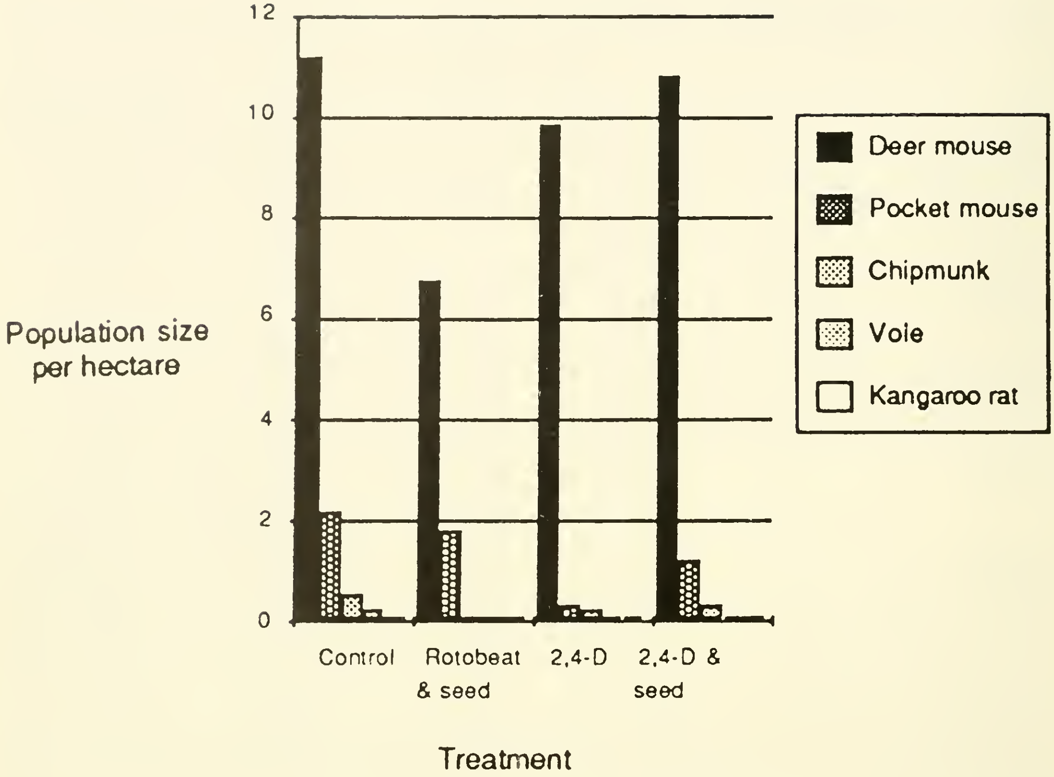

Fig. 3. Mean estimates of population density, for the summer season, for five rodent species in relationship to habitat treatment and control plots.

range of deer mice in control plots was smaller than in the treatment plots (F = 9.50, d.f. = 3.6, p = .011) (Table 3). No differences were found between the average size of home ranges for males and females (F = 0.00, d.f. = 2.0) as well as adult and juvenile deer mice (F = 0.70, d.f. = 2.0). Apparently, habitat treatments in this initial stage reduced the quality of the habitat for deer mice, and they responded by either increasing the size of their home range or by dispersing. A regression of home range size in relationship to population densities of the deer mouse showed a negative association on all plots (Fig. 5). This agrees with observations by Parmenter and MacMahon (1983) and Wolff (1984) that home range size of the deer mouse is a function of population density. Also, Taitt (1981) showed that home ranges of the deer mouse were smaller on food-supplemented grids than on control grids. O'Neal et al. (1987) found that the most reproductively successful pairs of kit foxes occupied the smallest home ranges in the best habitats.

In the described habitat manipulations, the vegetation reseeding effort must be considered a failure, as only a few seeds germinated and the seedlings quickly died in response to dry weather. Therefore, no reactions of rodents were considered related to seedlings, although rodents could have harvested some planted seed.

The ground cover (m^2/ha) of black sagebrush was 673 on control, 166 on the rotobeaten and reseeded, and 202 on the herbicide-treated plots. Data concerning the vegetative biomass present on different treatment and control plots for the three sampling periods showed distinct trends (Table 4). Shrub biomass differed significantly among treated plots and control plots (F = 11.34, d.f. = 2,4 p = .02) (Table 5). This variance was obviously expected as a result of the destructive nature of the perturbations on the treatment plots.

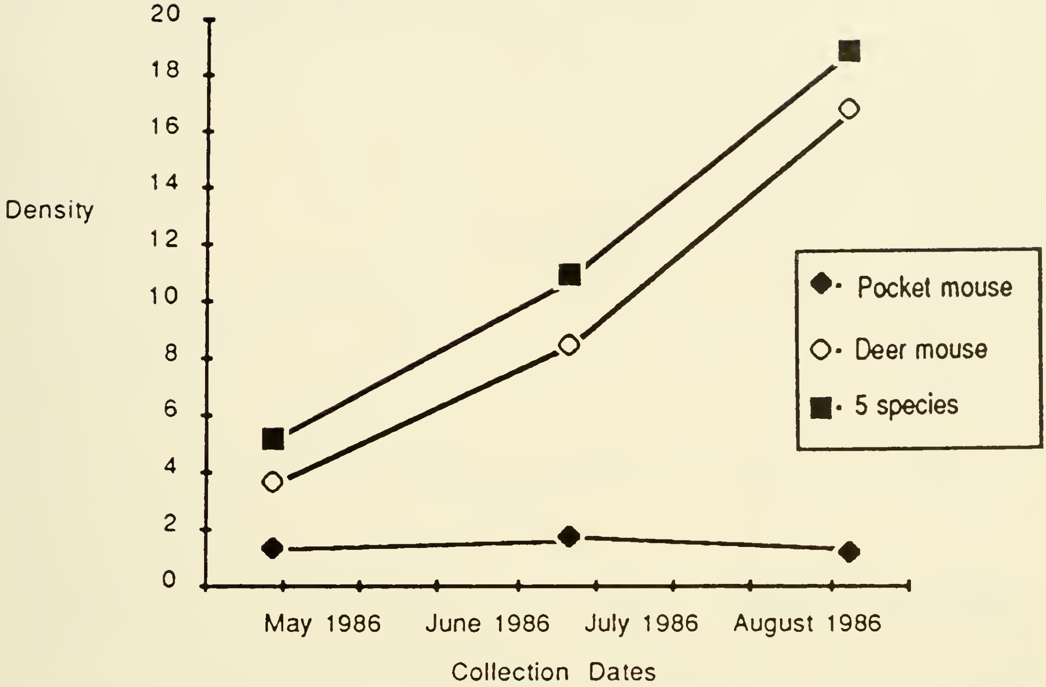

Fig. 4. Seasonal trend in estimated population density plotted for the deer mouse and Great Basin pocket mouse; values for the other three rodent species are combined.

TABLE 3. Differences in mean size of home ranges of the deer mouse on plots that received various habitat treatments in Garfield County, Utah.

Treatment	Home range ($\bar{x}$ ± SD)
Control	451 m^2 ± 416*a
Rotobeating and reseeding	1110 m^2 ± 1144b
Herbicide	1177 m^2 ± 863b
Herbicide and reseeding	709 m^2 ± 759a

*Values followed by different letters, a and b, are significantly different.

Grass biomass significantly increased on the herbicide treated plots (F = 79.18, d.f. = 2,4 p = .001), and this too was expected (Johnson 1964). There were no significant differences in forb biomass between the treatment and control plots (Table 5).

Percent frequency of occurrence for common plant species on treatment and control plots is shown in Tables 6, 7, and 8. Summarized data on frequency of occurrence for vegetation were submitted to cluster analysis (Sneath and Sokal 1973) (Fig. 6), and the following conclusions seem evident: (1) Seasonal changes in vegetation frequency were more evident than changes attributed to habitat treatments. (2) Although vegetation frequency varied among the treatment and control plots, there was usually at least 50% agreement. (3) Vegetation on the treated plots was more homogeneous and had greater congruity than vegetation on control plots.

Regression analysis suggests there was an inverse linear relationship (r = −.76) between the diversity of the frequency of occurrence for vegetation and the same diversity of rodents on the study plots (Table 9).

DISCUSSION

Because biomass of graminoides and annual forbs was less affected by habitat treatments than was biomass of shrubs, both grasses and forbs were more uniformly available as a food source for rodents on treatment and control plots. Biomass of grasses increased on plots treated by herbicide. Variation in plant species diversity on plots fails to account for rodent species diversity because the most vegetatively diverse plots had relatively lower rodent diversity (Table 9). This observation questions the relationship between plant

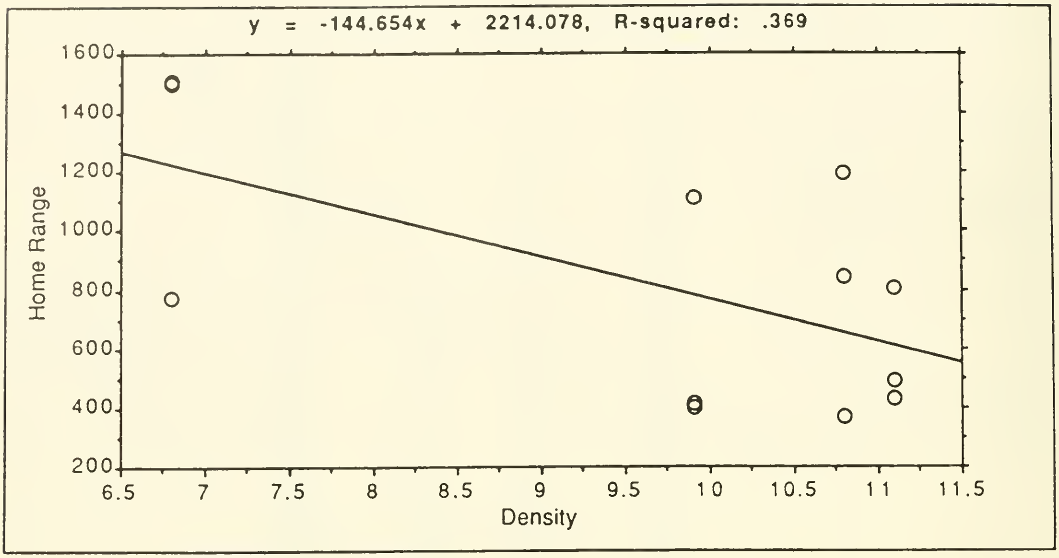

Fig. 5. Relationship of mean home range size to estimated population densities of the deer mouse for areas studied in relationship to habitat treatments.

TABLE 4. Mean vegetative biomass (kg/ha) for three sampling periods on plots studied in relationship to habitat treatments.

Species	May–July			July–August			August–September		
	Cont.	Roto.	Herbi.	Cont.	Roto.	Herbi.	Cont.	Roto.	Herbi.
Shrub									
x̄ ± SD	1247 ± 49	836 ± 226	330 ± 266	1162 ± 128	983 ± 157	555 ± 233	1074 ± 465	670 ± 270	683 ± 190
Grass									
x̄ ± SD	74 ± 60	65 ± 21	145 ± 52	68 ± 70	97 ± 63	170 ± 58	70 ± 57	64 ± 64	100 ± 25
Forbs									
x̄ ± SD	18 ± 16	4 ± 4	1 ± 1	17 ± 23	8 ± 13	1 ± 1	7 ± 6	2 ± 1	1 ± 1
Total									
x̄ ± SD	1339 ± 602	907 ± 417	477 ± 245	1247 ± 546	1089 ± 474	725 ± 274	1150 ± 569	737 ± 347	784 ± 269

TABLE 5. The mean vegetative biomass (kg/ha) data from three sampling periods during the summer of 1986 for plots studied in relationship to habitat treatments.

Treatment	Shrub x̄ ± SD	Grass x̄ ± SD	Forbs x̄ ± SD	Total x̄ ± SD
Control	1162 ± 253	71 ± 54	14 ± 5	1245 ± 557
Rotobeating and reseeding	830 ± 235	75 ± 56	5 ± 5	909 ± 388
Herbicide	523 ± 202	138 ± 49	1 ± 4	659 ± 253

species diversity and habitat complexity as discussed by Rosenzweig and Wineakur (1969).

Rotobeating and herbicide treatments severely changed cover aspects for resident small mammals, especially those aspects associated with woody vegetation. Loss of woody cover on treatment plots would contribute to increased xeric conditions for surviving plants and resident animals (e.g., arthropods and mammals), as well as reduced functional cover (e.g., hiding, nesting, and feeding) for small mammals. Arthropods are important dietary items for the deer mouse and, to a lesser extent, for the Great Basin pocket mouse and least chipmunk during the seasons of the year

TABLE 6. Percent frequency of occurrence for plant species during the first sampling period (May–early July) for treatment and control sites.

Species	Control	Rotobeating and reseeding	Herbicide	Herbicide and reseeding
Grasses				
Agropyron smithii	61	84	69	85
Sitanion hystrix	48	25	70	23
Shrubs				
Artemisia frigida	29	35	26	17
Artemisia nova	81	66	82	36
Artemisia pygmaea	11	1	1	2
Ceratoides lanata	69	57	74	39
Chrysothamnus depressus	19	2	6	1
Gutierrezia sarothrae	35	24	60	23
Leptodactylon pungens	12	0	0	0
Phlox hoodii	86	92	96	77
Tetradymia canescens	1	7	0	0
Forbs				
Arabis holboellii	7	0	0	0
Arabis pulchra	29	0	11	0
Chenopodium leptophyllum	1	1	4	0
Erigeron pumilus	24	7	24	2
Lesquerella ludoviciana	7	0	0	0
Melilotus officinalis	0	0	10	0
Phlox longifolia	26	6	14	13
Sanguisorba minor	0	0	19	3

TABLE 7. Percent frequency of occurrence for plant species during the second sampling period (July–early August) for treatment and control sites.

Species	Control	Rotobeating and reseeding	Herbicide	Herbicide and reseeding
Grasses				
Agropyron smithii	62	76	93	91
Elymus elymoides	6	0	0	1
Sitanion hystrix	37	28	23	20
Shrubs				
Artemisia frigida	33	29	41	29
Artemisia nova	58	62	54	48
Artemisia pygmaea	8	0	0	2
Ceratoides lanata	70	76	60	49
Chrysothamnus depressus	13	1	14	0
Chrysothamnus nauseosus	3	12	1	6
Gutierrezia sarothrae	30	41	30	30
Leptodactylon pungens	12	0	0	0
Phlox hoodii	89	92	90	71
Tetradymia canescens	0	3	4	2
Forbs				
Cordylanthus kingii	7	0	0	0
Erigeron pumilus	33	7	1	0
Phlox longifolia	2	10	4	13
Sanguisorba minor	0	4	0	1

covered by this study (Flake 1973, Thompson 1981). The prescribed habitat treatments could have negatively affected certain arthropod populations.

The removal of the shrubs through rotobeating and applications of 2,4-D caused no significant changes in the density of the deer mouse population during the first breeding season after treatment. Movements of several individuals between the treatment plots did not change the population distribution pattern. Home range size for deer mice differed

TABLE 8. Percent frequency of occurrence for plant species during the third sampling period (late August–September) for treatment and control sites.

Species	Control	Rotobeating and reseeding	Herbicide	Herbicide and reseeding
Grasses				
Agropyron smithii	70	93	97	99
Sitanion hystrix	30	19	13	13
Shrubs				
Artemisia frigida	36	40	22	13
Artemisia nova	91	81	62	47
Artemisia pygmaea	8	0	0	1
Ceratoides lanata	60	66	62	61
Chrysothamnus depressus	16	0	6	0
Chrysothamnus nauseosus	7	1	3	7
Gutierrezia sarothrae	43	50	24	24
Phlox hoodii	92	88	93	73
Forbs				
Arabis pulchra	8	1	0	0
Erigeron pumilus	22	3	1	0
Phlox longifolia	3	1	0	0

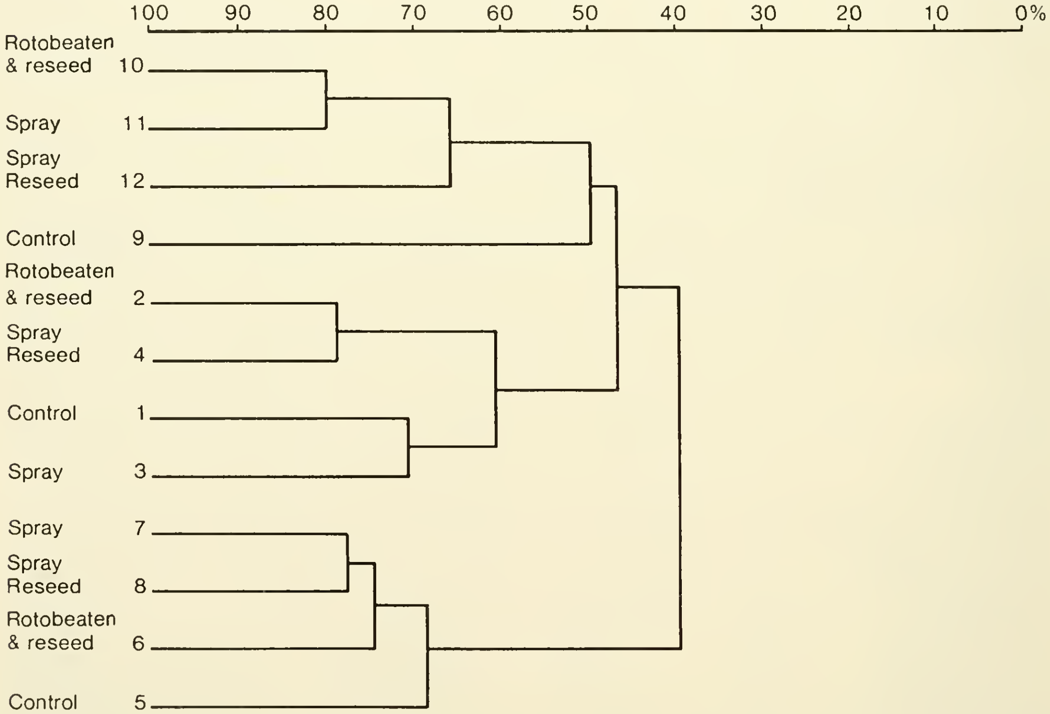

Fig. 6. Cluster analysis displaying the relationship between frequency of plant species occurrence on habitat treatment and control plots in southern Utah.

between the treatment and control plots. Home ranges were larger on rotobeaten plots than on those treated with herbicide. The smallest home ranges were found within the control plots. Deer mice are known to climb well and to successfully forage for arthropods and vegetation within the shrub canopy (Rosenzweig et al. 1975, Parmenter and MacMahon 1983, Kotler 1984). We must consider the area encompassed in the architecture of the shrub canopy as an extension of the home range of these rodents. Habitat perturbations

TABLE 9. Values for an index of diversity (MacArthur index, 1972) pertaining to frequency of occurrence for vegetation and five rodent species on plots studied in relationship to habitat treatments.

Treatments	Diversity of vegetation	Diversity of rodents
Control	9.1	1.3
Rotobeating and reseeding	6.5	1.6
Herbicide	6.6	1.5

that reduce this third dimension of area available for foraging may force resident deer mice to expand their two-dimensional home range. Rotobeating of shrubs would immediately reduce the canopy aspects of home range, while treatment with 2,4-D would have a more gradual effect. The arthropod population dependent on the shrub canopy would also be eliminated, thus forcing deer mice to forage for terrestrial arthropods, succulent vegetation, and seeds. This behavior would bring them into more direct conflict with resident pocket mice over use of these essential resources. Data indicate deer mice apparently dominate in these kinds of interactions. Brown and Munger (1985) showed that competition for limited food resources had a decided effect on organization of desert rodent communities. Species occupying different feeding and habitat guilds would not be expected to respond in a competitive manner (Hallet et al. 1982). Deer mice readily forage for seeds of grass, forbs, and shrubs (Everett et al. 1978) and thus have seriously contributed to failures of rangeland seedings (Howard 1950, Spencer 1954, Nord 1965, Nelson et al. 1970). Their contributions to the failure of the seeding efforts in this study are unknown, but population levels on the herbicide and reseeded plots remained near that of the control plots.

The rather severe habitat treatments negatively affected resident pocket mice (Table 1, Fig. 3). Following habitat treatments, interactions between pocket mice and deer mice for essential, but reduced, resources may have registered negative impacts on pocket mice. The mechanical disturbances of rotobeating and, to a lesser extent, herbicide treatment may have collapsed the shallow network of tunnels usually maintained by the Great Basin pocket mouse (Banfield 1974). A dense crown cover of vegetation prevents chilled air from settling to ground level at night (Smith 1966), and this would be most important for very small mammals occupying high, cold desert communities. Loss of functional cover would also increase the risk from avian and terrestrial nocturnal predators. Pocket mice are crepuscular and nocturnal and, thus, would be active concurrently with deer mice. Apparently the combination of factors associated with the prescribed habitat treatments negatively impacted these pocket mice (Table 1, Figs. 3, 4).

A certain threshold of shrub canopy cover is important for environmental amelioration for the diurnal least chipmunk (Parmenter and MacMahon 1983) and for protection from avian and terrestrial predators. The severe reduction in shrub canopy cover on the rotobeaten plots probably induced least chipmunks to emigrate to more favorable sites. They remained on the herbicide-treated plots until the third trapping period. Apparently the dead canopy of shrubs provided adequate cover until daily ambient temperatures reached their highest levels, thus forcing dispersal (Table 1). The fossorial behavior of least chipmunks (Lechleitner 1969) would substitute for some loss of shrub canopy cover but would not protect these rodents while foraging.

Sagebrush voles were uncommon and found only on rotobeaten plots during the first sampling period after treatment, thereafter being confined to the control plots. They have been observed to be active 24 hours of the day, year-round, and are considered strictly vegetarian (Carroll and Genoways 1980), preferring succulent vegetation such as tender leaves, nodes, young culms, and seeds in the dough stage (Maser et al. 1974). Sagebrush (usually *Artemisia tridentata*) leaves are heavily utilized from October through January; furthermore, sagebrush and rabbitbrush (*Chrysothamnus* sp.), either alive or dead, function as essential year-round cover (Maser et al. 1974). There is a negative relationship between wind velocity at ground level and activity of sagebrush voles aboveground (Maser et al. 1974). Therefore, treatments that reduced the aboveground vegetation would contribute to increased wind at the ground surface. The prescribed habitat treatments were detrimental to the short-term and long-term requirements of sagebrush voles (MacArthur 1972).

The overall plant community and rather heavy clay to stony soils on the study site are probably not ideal habitat for Ord's kangaroo rats. These nocturnal rodents are rather poor burrowers because of their weak forelegs and slender claws and are usually found in burrow systems dug in loose sand or loess (Banfield 1974). The process of rotobeating on plots often uprooted shrubs from the soil; this action created soil conditions more compatible with the requirements of kangaroo rats. The more xeric conditions created by this treatment were probably not detrimental to this desert-adapted species.

This study did not address other factors that could and, perhaps, did influence the populations of small mammals on the treatment and control plots. Beneficial data and insight could be gained from documenting direct behavioral interactions between species, determining the effects of disease and parasites, observing differential responses of predators, looking at unresolved mortality, documenting long-term reproduction and dispersal, and examining ecological relationships with the Utah prairie dog.

Funding constraints did not allow for a longer period of posttreatment investigation. We concur with Wiens and Rotenberry (1985) in appreciating that time lags in responses of individual animals on treated plots, as well as behavioral fidelity to sites regardless of treatments, make data from these kinds of studies more difficult to interpret.

CONCLUSIONS

Evaluation of field data in relationship to the working hypotheses provides useful insight for ecological studies that use experimental designs involving evaluations of treatment and control data. Results in our study were compromised somewhat by restricting the evaluation to the first season after habitat treatments, failure of the reseeding effort, and confounding by factors similar to those discussed by Wiens and Rotenberry 1985. A concise evaluation of these premises would include the following.

Hypothesis 1: Population densities of small mammals on treated plots would be reduced by a combination of factors including depressed reproduction, increased dispersal, and increased mortality. Our data on population density of the deer mouse and Great Basin pocket mouse did not support this assumption. Scanty data regarding least chipmunks and sagebrush voles seemed to agree with this premise. Seasonal trends indicated that reproduction of pocket mice and perhaps survival of juveniles were negatively affected by the prescribed habitat perturbations.

Hypothesis 2: The size of home ranges of the various rodent species would generally increase on treated areas. Trapping results provided significant data only for the deer mouse, and home ranges of these mice increased in size apparently in response to habitat treatments.

Hypothesis 3: Body weights of rodents, as an indicator of body condition, would be proportionately less on treated plots. Adequate data on the deer mouse did not validate this hypothesis. Habitat treatments did not limit food or the foraging capabilities of this opportunistic mouse.

Hypothesis 4: Diversity of the rodent species would decrease in relationship to vegetational treatments; interspecific dominance by one or more species may be evidenced. Lack of significant data on rodents other than the deer mouse weakens the conclusion that this premise is not true ($r = -.87$). The deer mouse appears to be interspecifically dominant in its guild and probably most affected the Great Basin pocket mouse on treated sites.

Hypothesis 5: The effects of vegetational treatments can be quantitatively measured and expressed in ways meaningful to those who investigate resident rodent populations. Measured reductions in canopy cover of shrubs on treated plots agreed with two-dimensional expansion of home ranges of the deer mouse. The canopy of shrubs serves as a third-dimension of foraging habitat for the deer mouse, and they respond to removal of this resource.

ACKNOWLEDGMENTS

We thank personnel of the Non-Game Wildlife and Game Management sections of the Utah Division of Wildlife Resources for significant monetary support and experimental counsel. Appreciation is extended to the U.S. Bureau of Land Management for use of comfortable living facilities while in the field.

Brigham Young University also provided critical monetary support. Dr. Samuel R. Rushforth provided expert counsel regarding cluster analysis. Gratitude is extended to James Mackley for helping with many aspects of the research and to Dale Thurber for assistance in trapping small mammals.

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EVALUATION OF WILDLIFE RESPONSE TO A RETAINED MINE HIGHWALL IN SOUTH CENTRAL WYOMING

John P. Ward[1] and Stanley H. Anderson[1]

ABSTRACT.—From 1984 through 1985 a study was made of the influence of a retained mine highwall on a wildlife community in south central Wyoming. Vegetation species richness and diversity were greater near the highwall compared with two adjacent sites 150 m in front of and behind the highwall. However, vegetation abundance (cover) was greater on the two adjacent sites. Small mammal abundance, richness, and diversity were greater on the highwall than on the two adjacent sites. Male bird abundance, richness, and diversity were greatest in front of the highwall (+50 m to +350 m) compared with the highwall and the area behind the highwall.

Current reclamation law mandates that operators reestablish the approximate original contour of mined lands (Surface Mining Control and Reclamation Act [SMCRA] 1977). Unless otherwise approved, operators are legally bound to regrade rills and gullies over 15.25 cm deep, fill surface depressions, and spread topsoil evenly on all affected lands. These practices result in a moderated topography with only the macrocontours restored (Tessman, Wyoming Game and Fish Department, personal communication). However, wildlife biologists recognize that such conditions may be insufficient to fulfill certain wildlife requirements including cover, shelter, and food. Therefore, some biologists now recommend regrading affected areas into minor hills and undulations sufficient to provide visual barriers, escape corridors, and increased habitat diversity. One reclamation alternative is the permanent retention of a final highwall. As mentioned above, SMCRA presently requires highwalls to be backfilled and leveled. In certain instances, raptors (especially Golden Eagles [*Aquila chrysaetos*] and Redtailed Hawks [*Buteo jamaicensis*]) have constructed nests on highwalls before reclamation was initiated (Fala et al. 1982). This may indicate that highwalls could improve wildlife habitation of an otherwise flat, homogeneous surface.

Considering this potential, the U.S. Office of Surface Mining (OSM) approved (13 May 1983) a variance request by Arch Mineral Corporation to leave a highwall segment on reclaimed surfaces near Hanna, Wyoming. This proposal was closely coordinated with the U.S. Fish and Wildlife Service and Wyoming Game and Fish Department and had the concurrence of both agencies.

The objective of the variance was to develop a study comparing wildlife use of the highwall with that of conventional reclamation from 1983 through 1985.

STUDY AREA

The highwall variance is located in south central Wyoming, 40 km east of Rawlins, Wyoming, and 16 km west of Hanna, Wyoming. This area, referred to as the Hanna basin, ranges in elevation from approximately 1,900 to 2,400 m. Vegetation is typical of the high, semiarid plains where sagebrush (*Artemisia* spp.) and grassland communities dominate. Greasewood (*Sarcobatus* spp.) prevails within ephemeral drainages (Fala et al. 1985). Grassland vegetation in the area includes *Artemisia* spp., *Chrysothamnus* spp., *Koeleria* spp., *Agropyron* spp., *Stipa* spp., and *Carex* spp. Sagebrush communities are composed of *Artemisia* spp., *Chrysothamnus* spp., *Atriplex* spp., *Sarcobatus* spp., *Agropyron* spp., *Poa* spp., *Sitanion* spp., *Carex* spp., *Hordeum* spp., *Elymus* spp., *Juncus* spp., *Oryzopsis* spp., and *Bromus* spp. Topography is gentle with dissecting drainage patterns and numerous rock outcrops. Winds are predominantly west to southwest. Occasional upslope winds from the south or east occur during winter.

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Highwall History

The area in which the highwall now exists was first mined from December 1977 to January 1978. The original highwall was approximately 30 m high and 1,000 m long. Reclamation began in June 1981, and the area was backfilled and regraded by June 1982. Because the highwall variance had not been approved by Wyoming's Department of Environmental Quality (DEQ) or the OSM, no topsoil was applied. On 4 March 1983 the DEQ officially approved the highwall variance, and on 13 May 1983 the OSM concurred. Topsoil was applied in June 1983. Disking, mulching, and seeding were completed the last week of October 1983.

The resulting highwall is approximately 10 m tall at the highest point and 425 m long. The general aspect is 196 degrees (south). Parent material is sandstone. The nearest natural cliffs are 2.7 km east and 4.2 km north.

The area in front of the highwall (south) gently slopes at a rise of 10 degrees in 158 m to the top of a contoured ridge. Immediately to the back side (north) of the highwall is a spoil bank 100 m long and 9 m high with a 25-degree embankment. North of the spoil bank is a contoured ridge that slopes at 6.5 degrees and extends the entire highwall length. Fourteen rockpiles have been placed in the highwall area. Ten of these are located along the base of the highwall. The remaining four rockpiles are dispersed on the upslope to the south. The farthest rockpile is 122 m south. The nearest undisturbed, contiguous sagebrush-grassland habitat is 75 m southwest of the highwall. Small patches of undisturbed vegetation occur in the rimrock 100 m north of the highwall. General drainage flows to the base of the highwall then westward.

The area south of the highwall was seeded in October 1983, and the area to the north was seeded in 1982. Seed was applied using both broadcast and drill methods. Seed that was drilled south of the highwall included (in kg/ha) western wheatgrass (*Agropyron smithii*) (3.93), thickspike wheatgrass (*Agropyron dasystachyum*) (3.93), slender wheatgrass (*Agropyron trachycaulum*) (2.24), bluebunch wheatgrass (*Agropyron spicatum*) (3.37), Indian ricegrass (*Oryzopsis hymenoides*) (1.12), and basin wild-rye (*Elymus* spp.) (1.68). Seed that was broadcast included winterfat (*Ceratoides lanta*) (0.56), rubber rabbitbrush (*Chrysothamnus* spp.) (0.28), and big sagebrush (*Artemisia tridentata*) (0.28). The area to the north was seeded with the same mixtures except that intermediate wheatgrass (*Agropyron* spp.) was substituted for bluebunch wheatgrass.

The area south of the highwall has also had some supplemental seeding. Twenty-three kilograms of sagebrush seed was hand-broadcast along the base and north-facing slope of the highwall. Also, 11 kg each of rabbitbrush and winterfat was broadcast in front of the highwall area.

METHODS

Small mammals were trapped 31 July–2 August 1984 and 28–30 July 1985. The sample design included three pairs of transects, each 210 m long. One pair (nos. 1 and 2) was 150 m in front of the highwall, another pair (nos. 5 and 6) was 150 m behind the highwall, and the third pair (nos. 3 and 4) was directly on the highwall. The pair on the highwall included one transect (no. 3) at the base and another (no. 4) at the top. When highwall ledges were present, traps of transect 3 were placed on the lower half of the highwall face. Similarly, traps of transect 4 were placed on the upper half of the highwall face. Eight trap stations were located at 30-m intervals. Each trap station included two aluminum box traps (23 × 9 × 8 cm) and two wire mesh traps (48 × 15 × 15 cm). One of each trap type was baited with sunflower seeds and the other with rolled oats. Traps were left open, baited for three consecutive nights, and checked twice daily—once in the morning (after sunrise) and once in the evening. Each small mammal captured was identified by species, age, and sex; it was then uniquely fur clipped and released. Small mammal abundance (number of newly captured small mammals), species richness (number of species), and species diversity [Shannon-Weiner function (Krebs 1978:455)] were determined for each transect pair.

Birds were sampled from the last week of May through 16 June each summer. One week prior to the sampling period, six 400-m transects were staked out on the study area. Three transects were located in front of the highwall and three behind it at distances of 50 m, 150 m, and 250 m. Wooden stakes were spaced at 100-m intervals along each transect, creating a 400 × 500-m grid. Bird transects were walked once a week for three consecutive weeks in the morning before 1000 hours. Locations of male birds (singing or calling) were plotted on a mylar sheet overlaid upon a schematic drawing of the area. The use of singing or calling males to estimate bird numbers is suited to territorial, noncolonial species (Bull 1981). This index has been used to make comparisons of bird use between areas or between years on the same area. After the field season each mylar sheet was overlaid with a scaled grid (700 × 500 m). All sightings were plotted on the grid, estimated to the nearest meter. Each bird was assigned to one of five quadrats. Quadrats 2 and 6 extended 150 m to 250 m in front of and behind the highwall face, respectively; quadrats 3 and 5 were 50 m to 150 m in front of and behind the highwall face, respectively; and quadrat 4 extended from 50 m in front of to 50 m behind the highwall face. Male bird abundance (total number of male birds counted), species richness (number of species), and species diversity [Shannon-Weiner function (Krebs 1978: 455)] were determined for each quadrat.

Vegetation was sampled at each small mammal trapping station. A 1-m^2 sampling frame partitioned by 25 evenly spaced points was randomly placed. The substrate directly under each of the 25 points was recorded. Soil was recorded as bare ground and vegetation was recorded by species. Vegetation abundance (number of plants counted) was tallied within each transect. Percentages of grasses, forbs, shrubs, and bare ground were calculated within each transect. Vegetation abundance, species richness (number of plant species), and species diversity [Shannon-Weiner function (Krebs 1978:455)] were determined for each transect pair.

TABLE 1. Average small mammal characteristics from 1984 and 1985.

	Transect pairs		
	1 and 2	3 and 4	5 and 6
Abundance	19.5	45.0	28.5
Richness	2.0	3.5	2.5
Diversity	0.12	0.18	0.13

TABLE 2. Small mammal species captured in 1984 and 1985. Numbers in parentheses represent 1985.

	Transect pairs		
Species	1 and 2	3 and 4	5 and 6
Deer mouse	17 (19)	36 (45)	19 (34)
Bushy-tailed woodrat		4 (1)	
Least chipmunk		1 (1)	
Silky pocket mouse			1 (2)
Striped skunk	0 (2)	0 (2)	1 (0)
White-tailed jackrabbit	1 (0)		

TABLE 3. Average male bird characteristics for 1984 and 1985.

	Quadrat number				
	2	3	4	5	6
Abundance	12.0	12.0	10.5	8.0	10.0
Richness	4.0	6.5	3.5	2.0	1.5
Diversity	0.47	0.75	0.42	0.16	0.05

RESULTS

Small mammal abundance and diversity were greatest on transect pair 3 and 4 compared with transect pairs 1 and 2, and 5 and 6 (Table 1). However, species richness was similar on all three transect pairs in 1984 and only slightly higher on transect pair 3 and 4 in 1985. Deer mice (*Peromyscus maniculatus*) were twice as abundant on transect pair 3 and 4 compared with transect pair 1 and 2, and 1.5 times more abundant compared with transect pair 5 and 6 (Table 2). Only one least chipmunk (*Eutamias minimus*) was captured each year. This species is diurnal and not susceptible to night trapping. Many were observed near transect pair 3 and 4, while none was observed near transect pairs 1 and 2, and 5 and 6.

On three occasions in 1984 and 1985 during small mammal trapping, a total of four pronghorned antelope (*Antilocapra americana*) were observed at the base of the highwall feeding or drinking from an intermittent pond that formed after heavy rainstorms. Numerous (~100) striped skunk (*Mephitis mephitis*) scats were found under three of the rockpiles, indicating use for cover.

Male bird abundance was generally greatest in front of the highwall on quadrats 2, 3, and 4 (Table 3). Species richness and species diversity were consistently greatest in quadrat 3, decreasing in quadrats 2, 4, 5, 6, respectively. Interestingly, a species composition shift appeared to occur from quadrat 2

TABLE 4. Male bird species observed in 1984 and 1985. Numbers in parentheses represent 1985.

	Quadrat number				
Species	2	3	4	5	6
Horned Lark	5 (9)	2 (2)	3 (8)	7 (7)	4 (15)
Mourning Dove	3 (2)	4 (1)	0 (1)	1 (0)	
Rock Wren	1 (0)	1 (3)	3 (4)		
Says Phoebe	1 (0)	3 (1)			
American Kestrel		1 (0)			
Brewer's Sparrow		0 (2)			
Mountain Bluebird	0 (2)	0 (1)	0 (1)	0 (1)	0 (1)
Brewer's Blackbird		0 (2)			
Sage Thrasher		0 (1)			
Violet-green Swallow		0 (1)			
Northern Harrier			0 (1)		

TABLE 5. Vegetation characteristics for transect pairs in 1985.

	Transect pairs		
	1 and 2	3 and 4	5 and 6
Abundance	281	162	209
Richness	3	10	5
Diversity	0.83	2.20	1.40

to quadrat 6 (Table 4). Although male bird abundance remained similar from quadrats 2 through 6, species richness decreased. Only one species [Horned Larks (*Eremophila alpestris*)] comprised the majority of birds seen on quadrat 6.

During the 1985 breeding season, one pair each of Mountain Bluebirds (*Sialia currucoides*), Violet-green Swallows (*Tachycineta thalassina*), Rock Wrens (*Salpinctes obsoletus*), and Mourning Doves (*Zenaida macroura*) nested in the highwall. However, we could document only that the Mountain Bluebirds and Mourning Doves successfully fledged young. One pair of American Kestrels (*Falco sparverius*) attempted to nest on the highwall in 1984, but a skull and bones found at the base indicated that one of the adults either was preyed upon or died of unknown causes.

Vegetation abundance (cover) was highest on transect pair 1 and 2 (Table 5). This was due primarily to the abundance of Russian thistle (*Salsola* spp.). Species richness and diversity were greatest on transects 3 and 4. Transect pair 3 and 4 also exhibited greatest evenness of thistle, grasses, and forb cover. The area with transect pair 5 and 6 was seeded one year before the other areas with transect pairs 1 and 2, and 3 and 4 (Table 6). Consequently, grasses were more established on transect pair 5 and 6, resulting in greater grass cover and reduced Russian thistle and hay cover. Seeding mixtures and planting techniques were similar on all three areas; therefore, similar revegetation trends should occur in future years. During rainstorms, we noticed that run-off accumulated at the base of the highwall. Vegetation response was visually apparent. Grasses, forbs, and some sagebrush seedlings had readily established in these areas compared with transect pair 1 and 2, which was planted at the same time.

DISCUSSION

Male bird diversity and small mammal diversity were greater nearer the highwall than the other two outlying areas sampled. This was both a direct and indirect result of the highwall's presence. Directly, the highwall provided secure nesting sites for at least five bird species (Rock Wren, Mourning Dove, Violet-green Swallow, Mountain Bluebird, and American Kestrel) and three den sites for mammal species [bushy-tailed woodrat (*Neotoma cinerea*), least chipmunk, and striped skunk]. Although the three mammal species, Rock Wren, and Mourning Dove are also found denning/nesting on other substrates (rimrock), the Violet-green Swallow, Mountain Bluebird, and American Kestrel would have been absent had the highwall been completely backfilled.

Biologists have documented other bird species nesting on unreclaimed highwalls, including Say's Phoebes (*Sayornis saya*) (Steele

TABLE 6. Vegetation composition of the highwall area in 1984 and 1985.

	Halogeton %	Thistle %	Grass %	Forbs %	Hay %	Soil %	Shrub %	Rock %
Transects 1 and 2								
1984	2.8	50.4	1.6	0.0	16.8	28.4	0.0	0.0
1985	0.3	58.2	5.0	0.0	6.8	29.7	0.0	0.0
Transects 3 and 4								
1984	6.0	40.7	3.6	0.0	0.0	49.7	0.0	0.0
1985	0.0	21.0	16.8	2.5	0.0	57.2	0.0	2.5
Transects 5 and 6								
1984	12.0	23.4	17.3	0.0	1.3	46.0	0.0	0.0
1985	9.5	0.0	42.5	0.0	0.0	47.5	0.5	0.0

and Grant 1982), Barn Swallows (*Hirundo rustica*) (Curtis et al. 1978, Northern Rough-winged Swallows (*Stelgidopteryx serripennis*) (Crawford et al. 1978), Eastern Phoebes (*Sayornis phoebe*) (Allaire 1978), Golden Eagles (*Aquila chrysaetos*) (Fala 1982), Prairie Falcons (*Falco mexicanus*) (Postovit and Postovit 1987), Great Horned Owls (*Bubo virginianus*) (Postovit and Postovit 1987), and Ferruginous Hawks (*Buteo regalis*) (Postovit and Postovit 1987).

The highwall in our study also provided cover to birds during adverse weather conditions. Shortly after a severe rainstorm, a pair of American Kestrels and one Great Horned Owl were flushed from the highwall, indicating that these two species used the highwall for protection. During the winter months two Golden Eagles and a Great Horned Owl frequently used the highwall for roosting (Ward and Anderson 1985).

Few studies have quantified use of highwalls by small mammals. However, numerous reports from Wyoming and Montana mines note mammal use of highwalls (D. Trueblood, Powder River Coal Company, Gillette, Wyoming, personal communication). Species and uses include: mule deer (*Odocoileus hemionus*) fawning, shade utilization, bedding, refuge from disturbance, and drinking; pronghorned antelope fawning and drinking; bushy-tailed woodrat, mountain cottontail (*Sylvilagus nuttalli*), and deer mice colonization; and red fox (*Vulpes fulva*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*) hunting and denning (D. Trueblood, Powder River Coal Company, Gillette, Wyoming, personal communication).

Bird and mammal diversity were also increased indirectly by the highwall. Typically, reclamation returns the land surface to "approximate" original contour, yielding a relatively flat topography. The highwall increased topographic diversity, thereby influencing surrounding soil, plants, and wildlife communities. Ward (1987) found more diverse soils and vegetation in areas associated with natural cliffs compared to flat, homogeneous, short-grass prairie. The diverse soils and vegetation afforded more habitat types, thereby supporting more bird and small mammal species. Grant et al. (1982) found that grassland small mammal community composition was determined by structural attributes. Grant et al. (1982) noted that as vegetation cover went from high to low on ungrazed grasslands, small mammal composition also decreased. Stah (1980) studied vertical structure of vegetation and coexistence of two *Peromyscus* species. She determined that because of the vertical stratification of the nesting location of these two species, there was enough niche separation to allow coexistence in the same habitat.

Anderson (1979) stated that habitat structure is the primary reason for the presence of birds in an open area. Bird species select habitats based on, among other things, the structural character of vegetation (Cullen 1957). Many preference studies have shown that height profile, or vertical structure, of vegetation is the primary predictor for bird species diversity (Cullen 1957, MacArthur and MacArthur 1961, Martin 1960, Krebs 1978). Horizontal stratification (patchiness) has been shown to be more important in determining bird species diversity in shrub and grassland habitat than in forested areas (Krebs 1978). However, Roth (1976) stated that bird species diversity may be predicted more accurately from a knowledge of both horizontal and vertical structure in the vegetation. Our results support Roth's findings. The highwall transects were characterized by greater vertical and horizontal structure and supported greater bird species diversity.

MANAGEMENT RECOMMENDATIONS

Before a mine manager proposes that a highwall be left as wildlife habitat, at least four questions must be addressed concerning the requirements of the wildlife species. (1) For what species of wildlife will the reclaimed area be managed? Some species (e.g., sage grouse, (*Centrocercus urophasianus*) may be adversely affected by the presence of a highwall. (2) Would the highwall provide habitat that is limiting to a target species? For example, scarcity of suitable nesting sites limits the local Golden Eagle population in the Hanna basin (Fala et al. 1985). Providing additional nest substrate could potentially increase the eagle population. (3) Are the target wildlife species found in the surrounding area? Birds will probably colonize a reclaimed highwall more readily than will mammalian species. For example, if there is not a local population of a particular small mammal in the area, the probability that this species will find and colonize the highwall is low. (4) If a highwall is designated for a particular species, can the design be altered to benefit other wildlife species without adversely affecting the targeted species. Data from other studies (Mosher and White 1976, McGahan 1968) indicate that Golden Eagles prefer south-exposed cliffs compared to north exposures, especially in cooler climates. Altering this exposure to benefit other wildlife species that prefer another exposure without adversely affecting the Golden Eagles may be possible.

Other questions to be addressed include the stability of the highwall's parent material, the landowner's desire or nondesire to have a highwall on his property, the safety considerations for humans and wildlife, and effects the highwall will have on aesthetics.

ACKNOWLEDGMENTS

S. Tessman and A. Anderson reviewed this manuscript. The Arch Mineral Corporation, Bureau of Land Management, Office of Surface Mining, Wyoming Game and Fish Department, and Wyoming Cooperative Fish and Wildlife Research Unit funded the project.

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EFFECTS OF ARTHROPODS ON ROOT:SHOOT RATIO AND BIOMASS PRODUCTION IN UNDISTURBED AND MODIFIED MOUNTAIN SHRUB HABITATS

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ABSTRACT.—In 1987 the effects of arthropods on root:shoot ratios and biomass production were examined in southeastern Wyoming mountain shrub habitats that were undisturbed or had undergone conventional shrub management by mowing, burning, or herbicide application during the previous year. In habitats with and without shrub canopy, treatment with insecticides generally increased foliage biomass and consistently decreased root biomass, regardless of the shrub management practice. In open areas the effects of insecticide treatments on the root and shoot biomass were relatively greater in undisturbed plots than in any of the managed plots. With only one exception, the root:shoot ratio increased following application of insecticide.

The dynamic balance between root and shoot biomass, termed a functional equilibrium by Brouwer (1963), responds to biotic and abiotic environmental changes. Plants of a specific age have a characteristic root:shoot ratio in a given environment and habitat (Crist and Stout 1929, Wareing 1970). In rangeland habitats, increases in root biomass may accompany increases in aboveground plant biomass (Weaver and Zink 1946). Shariff (1988) documented increases in both root and shoot biomass in sagebrush following disturbance of the habitat by burning. Walmsley et al. (1987) showed that the altered carbohydrate distributions within grasses defoliated by grasshoppers resulted in greater shoot biomass than root biomass. Leopold (1975) suggested that root growth is limited by the amount of carbohydrates produced from shoots, while shoots are limited by the availability of minerals from the root system. This concept was refined with the "sink and source" hypothesis of Neales and Incoll (1968).

Because sagebrush is considerably less palatable than many other range plants to cattle, burning, mowing, and herbicides are commonly used to rid areas of unwanted shrubs (Powell 1970). These chemical and mechanical defoliation practices can affect root-growth dynamics. A study by Shariff (1988) found that 2,4-D application and burning as management methods significantly increased sagebrush root biomass. However, an increase in root biomass may be short-term. Sturges (1980) found that the root biomass in the top 1.2 m of soil in a sagebrush habitat treated three years previously with 2,4-D was not significantly different from undisturbed areas.

Defoliation by arthropod feeding and by chemical or mechanical means may also induce changes in root:shoot ratios in mountain shrub habitats. The purpose of this research was to determine the effects of arthropods on root:shoot ratios and biomass production in undisturbed shrub habitats and those undergoing intensive vegetation modifications.

METHODS

This study was conducted on a Wyoming big sagebrush (*Artemisia tridentata wyomingensis* Nutt.) and antelope bitterbrush (*Purshia tridentata* [Pursh] D.C.) habitat located at an elevation of 2,400 m, 12 km southeast of Saratoga, Carbon County, Wyoming. The mean annual precipitation is 480 mm (mostly snow), and the mean annual temperature is 10.2 C. The daily mean temperature ranged from 21.0 to 27.0 C during the 100 days of the summer study period. The soils are brown sandy loams developed on loess, limestone, sandstone, and tuff of the North Park Formation. Limited grazing by roaming pronghorn antelope may have occurred during the study, but cattle were not present.

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In 1985 a botanical and pedological survey of the area was conducted (Powell, unpublished). Based on this work, we used sixteen 4-ha study plots that were randomly chosen from sites of similar vegetation, soil chemistry, and soil texture characteristics. Vegetation manipulations in May 1986 consisted of mowing four plots to a 20-cm stubble height, applying 2,4-D butyl ester in water at an aerial rate of 0.91 kg per hectare to four plots, and burning four plots. Four plots were left undisturbed as shrub management controls.

Two insecticides (carbaryl at 1.68 kg/ha and malathion at 1.4 kg/ha) were applied alternately every two weeks from early May through August 1987 to half of each managed and undisturbed plot. The other half of each plot was left as an untreated control. To determine effectiveness of insecticide treatments, we sampled the density of arthropods on foliage with a D-vac every 10 m along three 100-m transects in both closed (covered by shrub canopy) and open (not covered by shrub canopy) habitats in each half-plot every 10 days. The density of arthropods in litter was determined by collecting litter from 1-m^2 quadrats every 10 m along three 100-m transects in both open and closed habitats in each half-plot. Because the herbicide and burning virtually eliminated canopy cover, no samples could be obtained from closed habitats in these plots.

In August 1987 root biomass was determined by taking a 15-cm-deep and 10-cm-diameter core sample every 20 m along a 100-m transect, in 15 closed and open areas in each half-plot. On the same date, all herbaceous foliage was clipped from understory plants and overstory shrubs in 15 open and 15 closed 0.25-m^2 habitat quadrats located along three 100-m transects in each plot. Root core samples were first processed with a number 10 sieve and then with a number 18 sieve using water under pressure. Roots and foliage were dried at 75 C for three days and weighed.

Independent Students t-tests were used to determine differences in root and foliage biomass as a function of the insecticide treatments. A X^2 test of proportions was used to assess differences between root:shoot ratios as a function of insecticide treatments and shrub cover as a result of management practices.

TABLE 1. Effects of shrub management practices on sagebrush and bitterbrush canopy cover.

Management	% shrub cover[a]	
	1985 (premanagement)	1987 (postmanagement)
Undisturbed	28.1a	29.0a
Herbicide	29.6a	17.0b
Mowed	31.6a	23.0b
Burned	30.3a	6.2b

[a] Values within a management practice followed by different letters differ at the $P < .05$ level of significance according to the X^2 2 × 2 test of proportions.

RESULTS

All of the shrub management practices reduced ($P < .05$) the shrub cover (Table 1). Herbicide application and burning reduced shrub cover to the greatest extent; the shrub remaining after these management practices was dead and provided no distinct canopy. Because mowing left a 20-cm stubble of living shrub, a portion of the canopy remained intact. The canopy cover in undisturbed habitats did not change noticeably ($P > .05$) during the course of this study.

Insecticides reduced arthropod densities by 74–81% in the undisturbed and managed plots (Table 2). With one exception (undisturbed, closed habitats), application of insecticides to managed and undisturbed habitats significantly increased or decreased ($P < .05$) root:shoot biomass ratios, as compared to untreated controls (Table 3).

In open habitats of plots managed with the herbicide, insecticide application resulted in a 1.6-fold increase ($P < .05$) in foliage biomass and a 27% decrease ($P > .05$) in root biomass, as compared to untreated areas (Table 3). Ratio of roots to shoots decreased markedly ($P < .05$), reflecting the increase in shoot biomass after insecticide treatments.

Because mowing left a partial herbaceous canopy, the closed habitat was sampled. After application of insecticides to closed habitats, there was a 9.1-fold increase ($P < .05$) in shoot biomass and a 36% decrease in root biomass ($P > .05$), as compared to untreated areas. After insecticide applications in open areas, root biomass decreased markedly by 57% ($P < .05$) and shoot biomass decreased by only 6% ($P > .05$), compared to untreated plots. These effects were manifested by significant reductions ($P < .05$) in the root:shoot ratio, indicating a large shift toward production of shoot

TABLE 2. Effect of insecticide treatments on arthropod population densities ($no./m^2$) in undisturbed and managed plots.

Order	Habitat	Undisturbed		Mowed		Herbicide		Burned	
		con	trt[a]	con	trt	con	trt	con	trt
Acari	foliage	0	0	2	0	2	0	1	0
Araneae	foliage	6	1	3	0	3	1	5	2
Homoptera	foliage	218	41	31	6	33	2	21	4
Coleoptera	foliage	6	1	15	1	6	3	2	0
Diptera	foliage	13	2	3	0	2	1	3	1
Hymenoptera	foliage	64	10	73	29	80	20	13	1
Acari	litter	495	95	640	170	677	175	8	2
Araneae	litter	11	4	6	0	9	3	3	2
Homoptera	litter	14	3	11	2	10	2	3	1
Coleoptera	litter	13	0	9	0	10	2	1	1
Diptera	litter	24	5	13	1	27	9	12	5
Hymenoptera	litter	16	0	12	0	13	0	61	11
Collembola	litter	14	3	93	18	77	27	9	3
Thysanura	litter	6	1	8	0	3	0	1	0
% decrease			81%		75%		74%		77%

[a] con = control, trt = treated with insecticide.

TABLE 3. Root and foliage biomass and ratios as affected by insecticide treatments in undisturbed and intensively managed mountain shrub habitats.

Habitat	Management	Insecticide treatment	Biomass ($g/.25\ m^2$)[a]		Root:shoot ratio[b]
			Root	Shoot	
open	control	present	4.8 a	17.9 a	1:3 a
		absent	15.1 b	8.8 b	2:1 b
closed	control	present	7.6 a	32.8 a	1:4 a
		absent	10.0 a	47.3 b	1:5 a
open	mowed	present	2.8 a	8.1 a	1:3 a
		absent	6.5 b	8.6 a	1:1 b
closed	mowed	present	3.6 a	40.2 a	1:13 a
		absent	5.6 a	4.4 b	1:1 b
open	herbicide	present	6.5 a	13.3 a	1:2 a
		absent	8.9 a	8.5 b	1:1 b
closed	herbicide	present	NA[c]	NA	NA
		absent	NA	NA	NA
open	burned	present	1.1 a	11.5 a	1:11 a
		absent	2.3 a	8.2 a	1:4 b
closed	burned	present	NA	NA	NA
		absent	NA	NA	NA

[a] Means of foliage and root biomass within a habitat and shrub management practice followed by different letters differ at the $P < .05$ level of significance according to Students t-test.

[b] Root:shoot ratios within a habitat and shrub management practice followed by different letters differ at the $P < .05$ level of significance according to the X^2 2 × 2 test of proportions.

[c] The shrub management practice effectively eliminated the canopy, and so no closed habitats could be sampled.

biomass in both habitats after insecticide application (Table 3).

As with areas managed with herbicides, burned plots had essentially no live shrub canopy; thus, closed habitats could not be sampled. In open habitats of plots managed by burning, application of insecticide was associated with a 1.4-fold increase ($P > .05$) in foliage biomass and a 52% decrease ($P > .05$) in root biomass, compared to untreated controls. Although root and shoot biomass alone did not change significantly as a result of insecticide treatments, their combined effects resulted in a significant reduction ($P < .05$) in the root:shoot ratio, indicating an increase in the production of shoot biomass (Table 3).

Undisturbed plots that were used for assessing the role of arthropods in a natural sagebrush system clearly showed alterations in biomass production and root:shoot ratios following insecticide applications. In open areas treated with insecticides, there was a

2.0-fold increase ($P < .05$) in foliage biomass, with a 68% decrease ($P < .05$) in root biomass, compared to untreated controls. Insecticides applied to canopy-enclosed plots resulted in a 31% decrease ($P < .05$) in foliage biomass and a 24% decrease ($P < .05$) in root biomass. Root:shoot ratios reflect these changes, showing a significant shift ($P < .05$) toward shoot biomass production in open areas and a slight shift ($P > .05$) toward root biomass production in closed areas (Table 3).

Discussion

In our study all of the shrub management practices decreased root biomass relative to shoot biomass in open habitats. This result was opposite the results of Shariff's (1988) study on sagebrush habitats, which showed an increase in root biomass in managed areas. However, inasmuch as our study was conducted on the west slope and Shariff's (1988) study was performed on the east slope of the Medicine Bow Mountain range, environmental conditions were dissimilar. On the insecticide-treated plots there was generally a decrease in the absolute amount of foliage and a consistent increase in the absolute amount of root biomass. This trend was seen in the decreased root:shoot ratios following insecticide treatment in open and closed habitats, with all shrub management practices. We believe that arthropod activities (primarily feeding) influenced root and shoot biomass production in undisturbed and intensively managed mountain shrub habitats. These data do not entirely support the study of Walmsley et al. (1987), which found that while insect herbivory decreased foliage biomass, no clear differences in root:shoot ratios were evident three weeks after defoliation. Walmsley et al. (1987) conducted their study in the greenhouse using grasses fed upon exclusively by the migratory grasshopper *Melanoplus sanguinipes* (F.); therefore the study may not be comparable.

Accelerated shoot growth generally follows damage of foliage (Kleinendorst and Brouwer 1969), and this growth may partially compensate for the damage (Troughton, 1957). However, compensatory foliage growth can deplete carbohydrate reserves stored in the roots. This, in turn, may decrease root growth and root biomass (White 1973). These plant responses to herbivory are consistent with the root:shoot ratio and biomass production dynamics found in our study. A relatively higher root:shoot ratio may occur in habitats with limited resources (e.g., soil nutrients, light, and water), such as semiarid mountain shrub habitats. Conversely, an increase in shoot growth and biomass may be expected in habitats with abundant resources that permit maximum carbon gain through photosynthesis (Troughton 1977).

Grazing may also decrease root biomass by 60–70% relative to foliage biomass (Burleson and Hewitt 1982). However, this result was not observed in our study; root biomass was relatively greater in open areas (which were potentially exposed to grazing by pronghorn antelope and rodents) than in closed areas. However, the impact of grazing by vertebrates was confounded by different ecological factors in open and closed habitats; for example, grass foliage was more accessible in habitats without a shrub canopy.

The trends found in this study with regard to the role of arthropods in altering root:shoot ratio and biomass production were consistent across shrub management practices and habitats with the exception of closed areas in undisturbed plots. This exception, in which insecticides led to a significant decrease in foliage biomass, may have been a result of relatively poor penetration in insecticide in canopy-covered habitats. If the more mobile predators contacted the spatially limited insecticide more frequently than the herbivores, then there may have been a partial release of the herbivores from predation. Under these conditions a greater level of herbivory within the canopy may be expected.

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A NEW PERENNIAL SPECIES OF *GILIA* (POLEMONIACEAE) FROM UTAH

Frank J. Smith[1] and Elizabeth C. Neese[2]

ABSTRACT.—*Gilia tenuis* Smith & Neese is a previously undescribed species from Emery and Sevier counties, Utah, apparently closely related to *G. caespitosa* Gray and *G. subnuda* Torr. ex Gray. It is distinguished from these species by its possession of a combination of characters including perennial, multicipital habit, lobed basal leaves, and small, pale blue flowers.

Gilia tenuis Smith & Neese, sp. nov.

Species haec ab *Gilia caespitosa* Gray differt corollis sublazulinis corollae tubo angustis et foliis lobis; ab *G. subnuda* Torr. ex Gray differt corollis sublazulinis corollis parvis et habitu perenni.

Caespitose, perennial herb 5–15 cm tall from a woody-based, multicipital caudex, in age the plants mound-forming, the old stems clothed with marcescent leaf bases; herbage densely glandular puberulent throughout and with sand grains adhering; *leaves* principally basal, the basal ones crowded, 4–32 mm long, 1–7 mm wide, spatulate, obovate, or oblanceolate, irregularly toothed to pinnately lobed or a few sometimes entire, the lobes and apex broadly acute to obtuse or rounded and with an inconspicuous mucro, the cauline ones few, bractlike, to 18 mm long, mostly entire; *inflorescence* paniculate, openly branched from near base, the slender branchlets spreading-ascending; *flowers* perfect, borne in few-flowered, bracteate, cymose clusters near ends of branchlets, subsessile or with pedicels to 9 mm long; *calyx* 4–5 mm long, to 6 mm long in fruit, or (in late-season flowers) as short as 3 mm, exceeding the capsule at maturity, the lobes narrowly attenuate, about as long as tube, the lobes and midrib green, the intercostal membrane hyaline, ruptured by maturing capsule; *corolla* narrowly funnelform, delicate, concolorous, pale blue (yellowish in bud), glabrous or sparsely glandular, the tube 9–13 mm long and 1–3 mm in diameter, the lobes 4–6 mm long and 3–5 mm wide when well pressed; *filaments* short, unequally inserted in tube; anthers blue, the upper 3 clearly exserted but surpassed by corolla lobes, the lower two included and borne about midway in tube; *style* exserted, about equaling or slightly surpassing anthers; *capsule* ca 3 mm long; *seeds* about 2 mm long, few per capsule, narrowly elliptic or oblong, slightly mucilaginous when wet.

TYPE: USA, UT, SEVIER CO., head of Mussentuchit Creek, .9 mi (1.5 km) west of Emery Co. line, 6.8 air miles (11 km) south of Fremont Junction, T25S R5E S1 NW 1/4, at 1,900 m elevation; semibarren minor ridge of fine, pale sand, Dakota Formation, with scattered pinyon, juniper, and other "mound plants," 14 May 1987, *Elizabeth Neese, F. J. Smith, & Lisa Shaw 18025* (Holotype: BRY; isotypes: RM, NY, UC, UT, UTC).

PARATYPES: SEVIER CO.: head of Mussentuchit Creek, .9 mi (1.5 km) west of Emery Co. line, 6.8 air miles (11 km) south of Fremont Junction, T25S R5E S1 NW 1/4, at 1,900 m elevation, 3 June 1986, *Frank Smith & Lisa Shaw 2790* (UTC, NY); do, 10 August 1986, *Elizabeth Neese 17633* (BRY, NY, RM, PO); do, 1 July 1987, *Elizabeth Neese 18135* (MO, UC); T25S R5E S1 SW 1/4, on road to Last Chance Canyon, east side of Limestone Cliffs, 1,858 m elevation, 22 May 1987, *Kaye Thorne & Duane Atwood 5201* (BRY); do, 22 May 1980, *Duane Atwood 7516*. EMERY CO.: San Rafael Swell, T25S R8E S22; rim above (north of) Chimney Canyon, pinyon-juniper community, 1,800 m elevation, 22 May 1987, *Duane Atwood & Kaye Thorne 12709* (BRY); San Rafael Swell, 6,000 ft elevation, 6 June 1932, *Walter Cottam* (UTC).

Gilia tenuis occurs in south central Utah a short distance from the closely related, narrowly endemic *G. caespitosa*. Figure 1

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[1] 50 West 500 North, Logan, Utah 84321.

[2] Herbarium, University of California, Berkeley, California 94720.

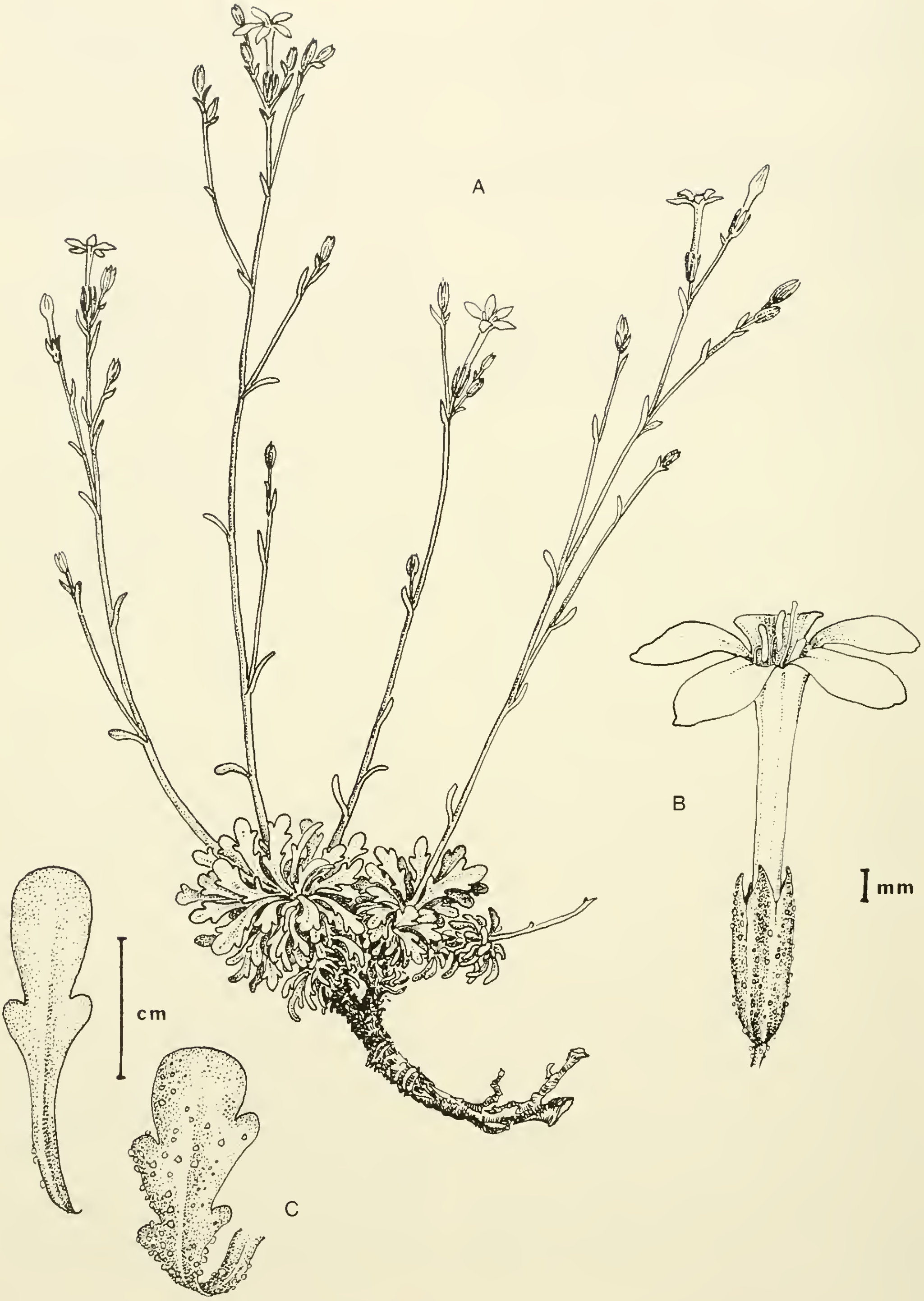

Fig. 1. *Gilia tenuis:* A, habit; B, flower; C, leaf close-up.

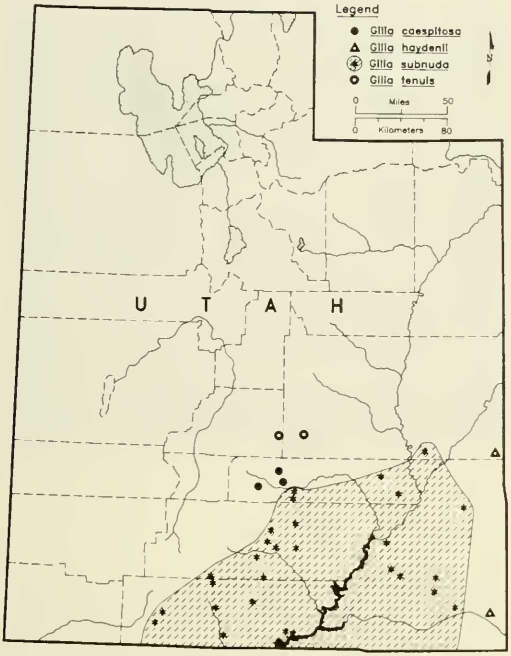

Fig. 2. Map showing distribution of *Gilia tenuis* relative to *G. subnuda*, *G. caespitosa*, and *G. haydenii* in Utah.

illustrates details of morphology and habit. Figure 2 shows the distribution of *G. tenuis* relative to the distributions in Utah of other members of the section *Giliandra*, with which it is allied (see discussion). *Gilia tenuis* occupies open habitats of pinyon-juniper woodland, where it grows on sparsely vegetated, fine-textured, pale, poorly cemented Jurassic and lower Cretaceous sandstones. The following key, which segregates *G. tenuis* from closely allied species that occur in Utah, is modified from the *Gilia* key in A Utah Flora (Welsh et al. 1987). It can be inserted on page 458 beginning with lead 10:

10(1). Plants perennial from a branching caudex 10a

— Plants annual or biennial, a caudex not developed 11

10a(10). Flowers red; plants from western Wayne County .... *G. caespitosa* Gray

— Flowers pale blue; plants from western Emery and eastern Sevier County .... *G. tenuis* Smith & Neese

11(10). Overall corolla length 1.5–4.5 cm or more .. 12

— Overall corolla length 0.2–1 cm ...... (to lead 15)

12(11). Basal leaves obovate-spatulate, merely dentate; corollas usually carmine; plants of southeastern Utah .... *G. subnuda* Torr. ex Gray

— Basal leaves variously shaped but definitely pinnatifid, flowers variously colored; distribution various 13

13(12). Basal leaves with a rachis 2–4 mm wide; flowers pink-purple (bluish on drying), funnelform, 1.5–2 cm long; plants of eastern Grand and San Juan counties .... *G. haydenii* Gray

— Basal leaves with the rachis commonly less than 2 mm wide; flowers scarlet, salmon, pink, white, or blue; distribution various .... (to lead 14)

DISCUSSION

The existence of this perennial *Gilia* was brought to our attention by a collection made during inventory of rare plant taxa occurring on lands administered by the Bureau of Land Management, Richfield District. Subsequent field investigation and examination of additional herbarium material show *Gilia tenuis* to occur in three small populations in the Muddy Creek and Last Chance Creek drainage system near the Emery/Sevier county line. The earliest known collection was taken from Emery County in 1932 by Walter Cottam, preeminent Utah ecologist and botanist whose collections span more than 50 years. That specimen, labeled simply "dry wash, San Rafael Swell" and identified only as "*Gilia*," was filed at UTC with specimens of *G. subnuda*. The taxon was again collected in 1980, when Duane Atwood and Bob Thompson took material (Atwood 7516, BRY) from Sevier County near Last Chance Creek (Duane Atwood, personal communication); that specimen, incorrectly labeled as being from Cathedral Valley, was also filed with *G. subnuda*. The taxon was independently discovered by the senior author near the head of Mussentuchit Creek, a small tributary of Last Chance Creek, during the 1986 rare plant study mentioned above; fruiting material was collected later that season and type material the following spring. Subsequent collections were made by Duane Atwood and Kaye Thorne from both the Last Chance Creek station and the west base of the San Rafael Swell overlooking Muddy Creek. The latter station may coincide with that of the early Cottam collection.

In populations we studied, a relatively small proportion of the plants form broad mounds that result from old and much-branched caudices. In young individuals the caudex remains unbranched and the plant simulates a taprooted biennial; this characteristic, in combination with the densely glandular, lobed, basal leaves, results in close superficial resemblance of some specimens of *Gilia tenuis* to red-flowered *G. subnuda*. However, it is well separated from that taxon (in addition to characters mentioned in the diagnosis) by the diminuitive habit, the slender stems, the delicate and less densely glandular corollas, and the exserted stamens. It is distinct from red-flowered *G. caespitosa*, in addition to characters given in the diagnosis, by its greater height, more open and freely branched inflorescence, and less densely caespitose habit. *Gilia haydenii*, also a member of section *Giliandra*, is a relatively robust biennial with pink-purple flowers known from a small area in southwestern Colorado and adjacent Utah and New Mexico. As shown in Figure 2, the distributions of *G. tenuis*, *G. caespitosa*, and *G. haydenii* occur near the periphery of the range of the more widely distributed *G. subnuda*. A fifth member of the alliance, *G. formosa* Greene, occurs 400 km to the southwest in San Juan County, New Mexico. It has relatively large, pinkish purple flowers and entire, acute leaves (the flowers of both *G. formosa* and *G. haydenii* become bluish on drying). *Gilia penstemonoides* Jones from west central Colorado shares with *G. tenuis* the characters of small blue flowers and perennial habit, but its affinities lie more toward *G. pinnatifida* Nutt. (Alva Day, personal communication). Additional collections and further study of the section *Giliandra*, most of whose members are uncommon and poorly known, are indicated.

The chromosome number of *Gilia tenuis* was determined to be 2N = 16. Anther squashes were made from flower buds collected at the type locality, fixed in Carnoy for 24 hours, and then transferred to 70% alcohol and stored at 4 C. Within *Gilia* this chromosome number has been reported for only five other taxa: *G. caespitosa*, *G. penstemonoides*, *G. pinnatifida*, *G. subnuda*, and *G. micromeria* Gray (Grant 1959, Wilken 1979). (Alva Day reports an unpublished count of 2N = 18 for *G. micromeria*.)

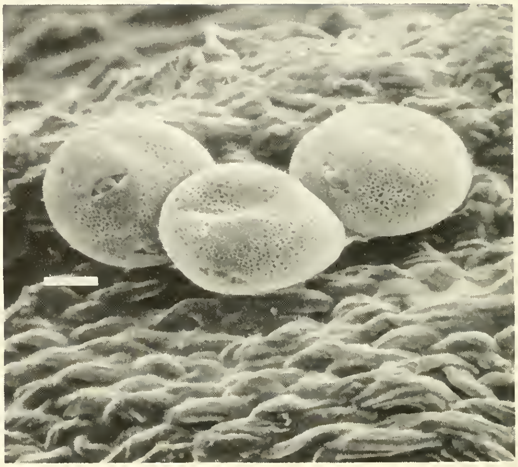

Fig. 3. *Gilia tenuis*: pollen grain. Bar = 10 μm.

Pollen for SEM micrographs (Fig. 3) was removed from anthers, air-dried, sputter-coated with Au/Pd for three minutes with a Polaron sputter-coater, and examined on an AMR–1000 SEM. *Gilia tenuis* has zonocolporate, reticulate grains as do *G. caespitosa* and *G. subnuda* (Stuchlik 1967, Wilken 1979). Most *Gilia* pollen grains are zonocolporate with either striato-reticulate or pertectate sexines (Taylor and Levin 1975).

Perennial and biennial species in the section *Giliandra* tend to be large, showy, and with well-exserted stamens, whereas smaller-flowered desert annuals in the section tend to be self-pollinated (Grant and Grant 1965). Although the flowers of *Gilia tenuis* are small and scarcely showy, the exserted stamens indicate that they are probably insect pollinated, and numerous bees and flies were observed visiting the flowers. Monitoring of insect visitors, including collection where possible, was conducted during early morning, at midday, and in late afternoon. Collections include *Lasioglossum* sp. (Halictidae), *Eupeodes volucris* (Syrphidae), and a number of unidentified members of the Anthomyiidae. An unidentified bee with a long proboscis (which may thus be a principal pollinator) was not captured but is believed to belong in the family Anthophoridae.

ACKNOWLEDGMENTS

This species came to our attention during floristic work funded by the Bureau of Land Management, Richfield District. We appreciate their support and assistance. Chromosome number determination was made by Catherine Hsiao, USDA-ARS, Forage and

Range, Utah State University. Insect visitors were identified by Dr. Wilford Hansen, Utah State University, and by Terry Griswold, USDA, Bee Biology and Systematics, Utah State University; SEM pollen micrographs were prepared in the Richards Memorial electron microscopy facility, Department of Biology, Utah State University, by William McManus. We gratefully acknowledge their assistance. We thank Drs. Duane Atwood, Arthur Cronquist, Alva Day, Leila Shultz, Stanley Welsh, and Dieter Wilken for comments. Kaye Thorne prepared the excellent illustrations.

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MARMOT SCATS SUPPLEMENT HAY PILE VEGETATION AS FOOD ENERGY FOR PIKAS

James A. Gessaman[1] and Andrew G. Goliszek[2]

ABSTRACT.—During summer pikas do not store fat for the winter months; hay piles are the main energy source in winter. All the hay piles collected in an area where pikas (*Ochotona princeps*) coexisted with marmots (*Marmota flaviventris*) contained marmot scats. Marmot scats had a higher energy density than the most abundant type of vegetation in hay piles.

In feeding trials pikas on a diet of hay pile vegetation plus marmot scats consumed significantly less food per day than they did on a diet of hay pile vegetation alone. These findings suggest that pikas coexisting with marmots use marmot scats to supplement the energy contained in the vegetational component of hay piles.

North American pikas (*Ochotona princeps*) gather meadow vegetation and store it in their talus territories during late summer and early fall (July–September). After this activity ceases, pikas continue to feed in meadows until snow covers the meadows, and then they feed under the snowpack on lichens and materials from their hay piles. Individuals usually construct several hay piles but do not cooperate with others in this construction. The hay piles gathered by an individual rarely contain sufficient energy or protein to provide adequate sole resources for surviving winter (Johnson and Maxwell 1966, Millar and Zwickel 1972, West 1980). Huntley et al. (1986) described factors that might cause this early termination of haying in the fall. In early spring hay piles may be critically important to individual survival because alpine conditions periodically prevent surface foraging and/or delay the emergence of new vegetative growth (Conner 1983).

Pikas, like other lagomorphs, are coprophagous. Besides ingesting their own caecal pellets, pikas have been observed collecting and eating the feces of animals with which they often coexist (Taylor and Shaw 1927, Broadbooks 1965, Elliott 1980). This observation suggests that feces as well as caecal pellets may be used by pikas as an added energy source in summer and winter.

In this study we measured food consumption rates of pikas fed hay piles with and without marmot scats, and the mass and energy content of vegetation and scats in hay piles at field sites with and without marmots. The fat content of pikas trapped in the spring and fall was measured to determine whether fat is stored before winter.

METHODS

We studied pikas in two rocky slope areas above 2,700 m in Cache County, Utah, about 56 km northeast of Logan. Area 1 contained populations of approximately 16 pikas and 12 marmots (*Marmota flaviventris*). Area 2 had a pika population of about 10 individuals, but no marmots. During 1979 and 1980 we located hay piles in areas 1 and 2, and marmot scats and vegetation in the hay piles were weighed at the end of the haying season. The most common materials in the hay piles were identified and their energy density measured with a Parr microbomb calorimeter (Model 1411).

The fat content of 10 pikas snap-trapped in 1980 was measured by fat extraction (Bligh and Dyer 1959). Two pikas were live-trapped in June 1980 and were caged separately indoors at 24 C on a light:dark schedule of 14:10. Food consumption of each pika was measured in nine feeding trials, each lasting 10 days. The diet alternated from trial to trial between: (1) 300 g dried vegetation (120 g grasses; 180 g *Rubus*, *Populus*, *Senecio*, and *Solidago*) and (2) 225 g dried vegetation (85 g grasses; 140 g *Rubus*, *Populus*, *Senecio* and *Solidago*) plus 75 g marmot scats. Hay piles in the feeding trials were constructed to simulate hay piles in the natural habitat. Weight of hay pile

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TABLE 1. Weights and energy content of pika hay pile components during fall 1979 and 1980 in study areas 1 and 2.

			Vegetation		Scats	
Study area	No. of hay piles	Year	Wt (g)	Energy content (kcal)	Wt (g)	Energy content (kcal)
1	12	1979	2,026 ± 975[1]	8,104 ± 3,900	992 ± 639	4,662 ± 3,003
	10	1980	2,256 ± 918	9,024 ± 3,672	412 ± 280	1,936 ± 1,316
			$\bar{x}$ = 2,141	$\bar{x}$ = 8,564	$\bar{x}$ = 702	$\bar{x}$ = 3,299
2	8	1979	5,175 ± 613	20,700 ± 2,452		
	5	1980	4,450 ± 596	17,800 ± 2,384		
			$\bar{x}$ = 4,813	$\bar{x}$ = 19,250		

Differences between hay piles in areas 1 and 2 for both years are significant at the 5% level

[1] (± SD).

consumed was measured at the end of a trial. The ratio of vegetation to scat consumed was not measured. Water was given ad libitum.

RESULTS AND DISCUSSION

Pikas began to gather hay piles in both areas in early August 1979 and 1980. Types of vegetation in hay piles from both areas were similar. We have no explanation for the absence of marmots in area 2. In area 1 marmot scats were dispersed throughout the hay piles, and hay piles were significantly smaller than those in area 2 (Table 1). The average weight of vegetation in hay piles in area 1 over two years was less than 45% of the average weight of vegetation in hay piles in area 2. All the hay piles collected in area 1 contained scats; 3 of 22 hay piles had more marmot scats by weight than vegetation. Marmot scats comprised, on average, 49% by weight of hay piles in area 1 in 1979 and 18.2% in 1980. Elliott (1980) found that marmot scats comprised 6% by weight of pika hay piles in Payette National Forest; he suggested that they are utilized as an auxiliary source of protein. Marmot scats had higher energy density (4.7 kcal/g) than grasses, the most abundant type of vegetation in hay piles (3.9 kcal/g). The average energy density of vegetation in hay piles was 4 kcal/g. The average energy content of hay piles (vegetation and scats) in area 1 was about 62% of that in hay piles area 2 (Table 1). Scats made up 27% of the energy content of hay piles in area 1. It is not clear why the average energy content of a hay pile in area 1 was significantly less than in area 2. The quantity and quality of vegetation in the two areas were not measured, but the quantity appeared very similar. The relative importance of scats and vegetation as sources of dietary energy is not apparent from these data because the metabolizable energy (the energy available from the food for maintenance and production) of these two dietary components is unknown.

Two pikas on a diet of hay pile vegetation plus marmot scats consumed significantly less food per day than they did on a diet of hay pile vegetation alone. On a diet of vegetation alone the average consumption rate for both pikas in the feeding trials was 18.9 g/day; 7–12 g/day lower than the food consumption rate reported by Millar and Zwickel (1972) for six captive pikas. On a diet of vegetation and marmot scats the average consumption rate of hay pile material for both pikas dropped 16%. Both pikas ate marmot scats; scat intake was observed more frequently at the end of the 10-day trials when hay piles were nearly depleted. Pikas must have obtained some of their daily maintenance energy requirements from ingested marmot scats because their body weight at the beginning and end of a feeding trial differed by less than 1%.

Body fat contents (% of body DM) of 5 pikas (3 male, 2 female) in the first week of June (6.4% ± 1.0%) and that of 5 pikas (3 male, 2 female) in late September–early October (6.7% ± 2.2%) were not significantly different ($\bar{x}^2 = 0.1$; $p > .5$).

CONCLUSION

Pikas do not store fat during the summer; therefore, hay piles are a very important energy source in winter for this nonhibernating species. Our field observations and feeding trials suggest that pikas coexisting with marmots use marmot scats to supplement the energy contained in the vegetational component of hay piles. Studies of the metabolizability of vegetation and scats, and the relative feeding preference of pikas for vegetation and scats are needed to determine the relative importance of scats as an energy source.

ACKNOWLEDGMENTS

This research was supported in part by a grant-in-aid from the Sigma Xi Research Society. We thank Emily C. Oaks and John C. Malechek for their help and encouragement during this study.

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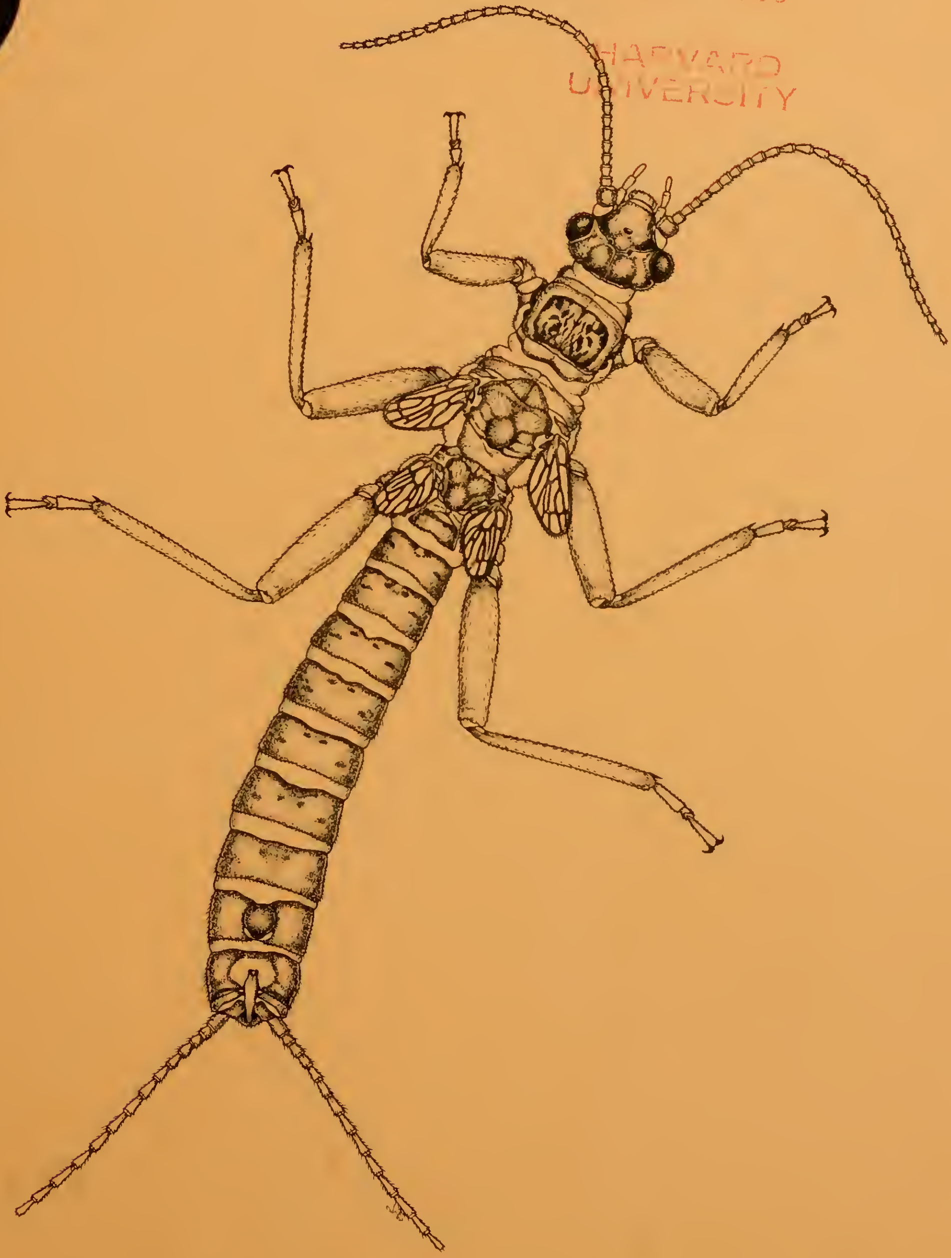

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12-89 650 43204

ISSN 017-3614

The Great Basin Naturalist

Published at Provo, Utah, by
Brigham Young University

ISSN 0017-3614

Volume 49 31 October 1989 No. 4

SOIL CHARACTERISTICS OF MOUNTAINOUS NORTHEASTERN NEVADA SAGEBRUSH COMMUNITY TYPES

Mark E. Jensen[1]

Abstract.—Soil physical and chemical properties were studied to identify habitat differences among 15 sagebrush-dominated plant community types of the Great Basin. The sagebrush taxa studied followed an apparent gradient of increasing soil fertility, with *Artemisia nova* commonly occupying the lowest fertility sites. Sites of moderate soil fertility tended to support *A. arbuscula*, *A. longiloba*, and *A. tridentata* ssp. *wyomingensis*. *Artemisia tridentata* ssp. *tridentata* and *A. tridentata* ssp. *vaseyana* were commonly found on sites with the highest soil fertility levels as indicated by maximum organic carbon, nitrogen, and phosphorus levels within such soils. Mollic epipedon depth, total depth, and water-holding capacity of the soil also increased as the dominant sagebrush taxon of a community type changed from *A. nova* to *A. tridentata* ssp. *vaseyana*. Data from this study provide information concerning soil relationships within relatively undisturbed rangeland communities. Such data are required if future soil sampling efforts within the Great Basin are to have a basis for comparison.

Distinct sagebrush (*Artemisia*)-dominated plant communities occur throughout the Great Basin region (Mooney 1985, Tueller and Eckert 1987). Such communities frequently occupy similar topographic and climatic settings, which suggests that soil factors may be controlling their distribution on the landscape (Young et al. 1985). Inasmuch as the various species and subspecies of *Artemisia* (Beetle 1960, McArthur 1979, Winward 1980) are commonly used to infer site environmental conditions in wildland management (Winward 1983), it is important that soil-plant community relationships be documented for these lands.

The mountainous rangelands of the Humboldt National Forest, northeastern Nevada, provide some relatively undisturbed expressions of sagebrush plant communities found throughout the Great Basin. The 15 sagebrush community types of this national forest (Jensen et al. 1988) are dominated by one of the following sagebrush taxa: *Artemisia nova* (ARNO), *A. arbuscula* (ARAR), *A. longiloba* (ARLO), *A. tridentata* ssp. *tridentata* (ARTR), *A. tridentata* ssp. *wyomingensis* (ARWY), and *A. tridentata* ssp. *vaseyana* (ARVA). This paper presents differences in site, soil physical, and soil chemical properties between those community types. Such information is essential if plant community type classifications are to be effectively utilized in resource assessment efforts by wildland managers.

Methods

Vegetation and soil data were collected on 372 relatively undisturbed, sagebrush-dominated rangeland sites of the Humboldt National Forest, northeastern Nevada (Fig. 1). Criteria for site selection and the vegetation sampling methods employed have been described previously (Jensen et al. 1988). Sites were located to reflect the best available

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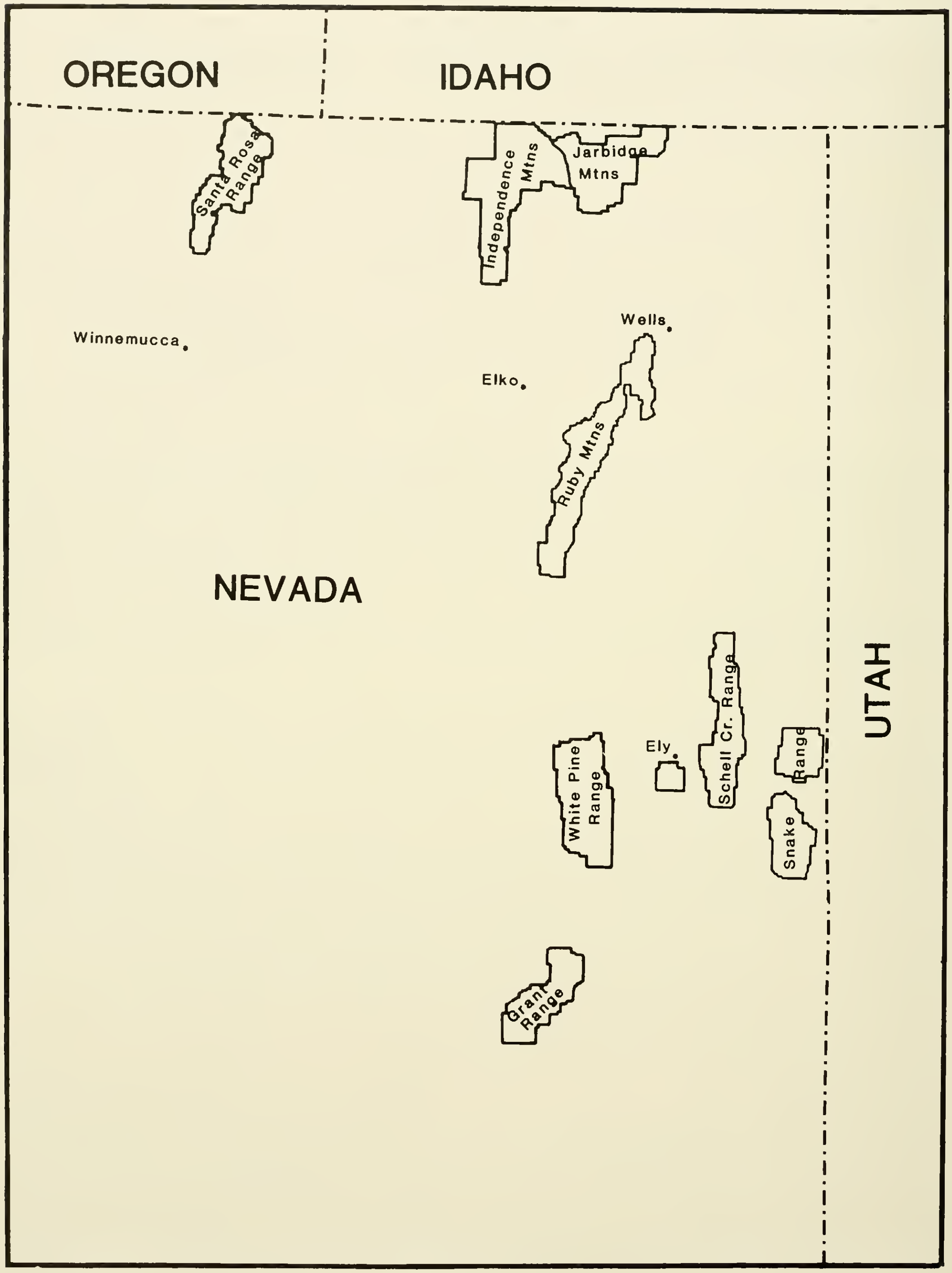
OREGON
IDAHO
Santa Rosa Range
Independence Mtns
Jarbidge Mtns
Wells
Winnemucca
Elko
Ruby Mtns
NEVADA
UTAH
Schell Cr. Range
Ely
White Pine Range
Range
Snake
Grant Range

Fig. 1. The Humboldt National Forest of northeastern Nevada.

expression of the potential natural community of an ecological site (Range Inventory Standardization Committee 1983).

Complete soil descriptions were made at each site to a depth of 1.5 m or, if present, to a shallower restrictive layer (e.g., lithic contact, petrocalcic horizon). Soils were classified to the family level of Soil Taxonomy (USDA 1975). Composite soil samples were collected for chemical and particle size analyses at each pedon at depths of 0–15 and 40–60 cm.

Soil analysis procedures employed follow Page et al. (1982). The following analyses were performed on each soil sample: pH (1:2 soil to water ratio), extractable phosphorus (sodium bicarbonate method), extractable bases (1 *N* ammonium acetate extraction with atomic absorption spectrophotometry analysis), organic matter (Walkley-Black method), total soluble salts (electrical conductivity method), cation exchange capacity (1 *N* ammonium acetate extraction), total nitrogen (micro-Kjeldahl method), extractable zinc and iron (DTPA method), calcium carbonate equivalent (gravimetric method), and particle size distribution (hydrometer method).

The following soil physical properties were recorded in the field and entered into a data file by A, B, and C master horizons for analysis: root abundance, texture, clay content (%), gravel, cobble, stone, and boulder content (% by volume), total rocks (%), mollic epipedon thickness, and horizon thickness. Site estimates of slope, aspect, elevation, rock type, infiltration, permeability, drainage, depth to restrictive layer, total water-holding capacity, erosion hazard, and compaction were also recorded for analysis.

Statistical analyses utilized programs contained in the Statistical Package for the Social Sciences (Norusis 1985).

RESULTS AND DISCUSSION

Soil Classification, Site, and Soil Physical Property Relationships

The sagebrush community types (C.T.) studied (Table 1) display noticeable differences in site and soil physical properties (Tables 2, 3). Sites with *A. nova* (ARNO) as the dominant sagebrush species have minimally developed mollic epipedons, if present, and belong primarily to the soil order Aridisol. The principal soil great groups associated with the ARNO/ATCO/SIHY, ARNO/ORHY, and ARNO/AGSP C.T.s are Haplargids, Paleorthids, and Calciorthids, respectively. Mollic epipedon thickness of the other community types is sufficient for classification of their soils in the order Mollisol. The ARAR/FEID, ARAR/FEID/POSA, and ARLO/FEID C.T.s are found primarily on Argixerolls, with Haploxerolls supporting most of the ARTR/AGSP, ARTR/FEID, and ARWY/SIHY C.T. sites. Sites with *A. tridentata* ssp. *vaseyana* (ARVA) as the dominant shrub (e.g., ARVA/AGSP, ARVA/SYOR/BRCA C.T.s) occur mainly on Cryoborolls.

The average mollic epipedon thickness of C.T.s dominated by *A. tridentata* ssp. *tridentata* or *vaseyana* (ARTR, ARVA) tends to be significantly greater than that of C.T.s dominated by *A. arbuscula* (ARAR), *A. longiloba* (ARLO), or *A. tridentata* ssp. *wyomingensis* (ARWY). Community types dominated by *A. nova* (e.g., ARNO/ORHY) have significantly shallower mollic epipedons than C.T.s with other sagebrush species. Within a given C.T. series (e.g., ARVA), sites with *Agropyron spicatum* (AGSP) as the primary grass species

TABLE 1. List of sagebrush community types identified on the forest (Jensen et al. 1988) and abbreviated codes referred to in the text.

ARNO/ATCO/SIHY	*Artemisia nova/ Atriplex confertifolia/ Sitanion hystrix*
ARNO/ORHY	*A. nova/Oryzopsis hymenoides*
ARNO/AGSP	*A. nova/Agropyron spicatum*
ARAR/AGSP	*A. arbuscula/Agropyron spicatum*
ARAR/FEID/POSA	*A. arbuscula/Festuca idahoensis/ Poa sandbergii*
ARAR/FEID	*A. arbuscula/Festuca idahoensis*
ARLO/FEID	*A. longiloba/Festuca idahoensis*
ARWY/SIHY	*A. tridentata* ssp. *wyomingensis/ Sitanion hystrix*
ARTR/AGSP	*A. tridentata* ssp. *tridentata/ Agropyron spicatum*
ARTR/FEID	*A. tridentata* ssp. *tridentata/ Festuca idahoensis*
ARVA/AGSP	*A. tridentata* ssp. *vaseyana/ Agropyron spicatum*
ARVA/FEID	*A. tridentata* ssp. *vaseyana/ Festuca idahoensis*
ARVA/ELCI	*A. tridentata* ssp. *vaseyana/ Elymus cinereus*
ARVA/SYOR/AGSP	*A. t.* ssp. *vaseyana/ Symphoricarpos oreophilus/ Agropyron spicatum*
ARVA/SYOR/BRCA	*A. t.* ssp. *vaseyana/ Symphoricarpos oreophilus/ Bromus carinatus*

TABLE 2. Listing of site and soil physical properties by sagebrush community type.

	Community type							
Property	ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWY SIHY
A HORIZON PROPERTIES	n = 12	n = 16	n = 44	n = 27	n = 19	n = 19	n = 4	n = 4
Depth (cm)	27 (17)	18 (10)	25 (10)	26 (17)	23 (8)	25 (9)	25 (10)	27 (10)
Dominant texture class	SL	SL	L	L	SiL	L	SiL	SL
Clay (%)	15 (4)	17 (7)	17 (3)	20 (4)	20 (5)	20 (5)	22 (5)	16 (9)
Gravel (%)	18 (11)	20 (10)	20 (9)	19 (10)	16 (7)	20 (11)	18 (3)	10 (4)
Total rock (%)	35 (15)	30 (10)	29 (11)	34 (11)	26 (9)	22 (10)	26 (10)	15 (7)
Water-holding capacity (cm)	2.5 (1.5)	2.0 (1.3)	3.4 (3.4)	2.8 (1.5)	2.8 (0.8)	3.3 (1.5)	3.5 (1.6)	3.0 (1.5)
SUBSOIL PROPERTIES								
Depth (cm)	44 (24)	42 (26)	51 (30)	40 (25)	43 (26)	38 (20)	56 (16)	66 (28)
Dominant texture class	SL	L	L	SCL	CL	SCL	CL	SCL
Clay (%)	18 (10)	21 (12)	20 (6)	28 (9)	32 (10)	30 (16)	33 (8)	24 (16)
Gravel (%)	14 (10)	21 (10)	22 (10)	20 (12)	17 (13)	22 (13)	14 (5)	18 (16)
Total rock (%)	38 (20)	42 (13)	45 (15)	44 (20)	39 (17)	32 (17)	30 (21)	37 (23)
OTHER PROPERTIES								
Depth of fine roots (cm)	22 (8)	20 (12)	25 (12)	24 (10)	21 (7)	25 (8)	18 (8)	30 (15)
Depth where 80% of roots end (cm)	42 (19)	35 (10)	39 (13)	38 (13)	34 (13)	35 (10)	29 (4)	38 (17)
Mollic epipedon depth (cm)	---	---	16 (16)	26 (9)	22 (9)	28 (9)	29 (4)	28 (38)
Soil depth (cm)	90 (32)	77 (28)	82 (32)	73 (26)	71 (28)	73 (26)	81 (26)	99 (37)
Total water-holding capacity (cm)	6.4 (2.8)	6.6 (2.8)	8.1 (5.3)	7.4 (3.8)	8.0 (3.6)	8.4 (3.8)	10.7 (4.1)	7.6 (3.3)
Slope (%)	24 (20)	15 (11)	20 (13)	24 (13)	13 (10)	13 (9)	6 (3)	4 (2)
Elevation (m)	1981 (118)	2091 (282)	2311 (292)	2403 (217)	2060 (380)	2061 (174)	1874 (72)	1950 (132)

have significantly thinner mollic epipedons than those with *Festuca idahoensis* (FEID).

The trends outlined above regarding differences in mollic epipedon thickness across the C.T.s also apply to total water-holding capacity and depth of the soil (Tables 2, 3). In general, C.T.s with *A. tridentata* ssp. *vaseyana* or *tridentata* as the dominant sagebrush species have significantly greater soil water-holding capacities and depth than those with *A. nova*, *A. arbuscula*, *A. longiloba*, or *A. tridentata* ssp. *wyomingensis* as the dominant shrub.

Clay content of both the A horizon and the subsoil at a site tend to be greatest for C.T.s dominated by *A. longiloba* or *A. arbuscula* (Tables 2, 3). These C.T.s frequently occur on soils that have well-developed argillic horizons and belong to fine-soil families (e.g., Aridic Palexerolls, fine, montmorillonitic, mesic). Such argillic horizons have been found to limit the effective rooting depth of a soil (Lentz and Simonson 1987).

Subsoil rock fragment content tends to be lowest on ARTR/FEID and ARTR/AGSP C.T.s. Significantly greater rock fragment contents are found within soils of C.T.s dominated by *A. tridentata* ssp. *vaseyana*. These soils frequently belong to skeletal soil families (e.g., Typic Cryoborolls, loamy-skeletal, mixed; Pachic Cryoborolls, loamy-skeletal, mixed) in the study area.

Hironaka et al. (1983) suggest that the distribution of sagebrush species is controlled primarily by the available soil moisture present at a site. They state that *A. nova* and *A. arbuscula* occupy the driest soil environments in Idaho because they are commonly found on soils that are shallow (i.e., less than 50-cm depth) or, if moderately deep, have a restrictive layer. These same species occupy much deeper soils in this study (Tables 2, 3); yet the average soil depth exploited by plant roots within ARNO and ARAR C.T.s is significantly shallower than those of the ARTR or ARVA C.T.s (Table 3).

TABLE 2 continued.

	Community type						
Property	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
A HORIZON PROPERTIES	n = 6	n = 8	n = 63	n = 67	n = 9	n = 23	n = 47
Depth (cm)	47 (27)	34 (19)	31 (15)	32 (14)	34 (16)	34 (15)	41 (17)
Dominant texture class	L	SiL	L	L	L	SiL	L
Clay (%)	18 (4)	20 (5)	17 (3)	17 (3)	18 (4)	18 (5)	17 (3)
Gravel (%)	18 (18)	21 (23)	19 (11)	20 (13)	23 (11)	16 (9)	22 (13)
Total rock (%)	25 (16)	22 (12)	32 (15)	23 (14)	28 (11)	27 (12)	25 (13)
Water-holding capacity (cm)	5.6 (4.3)	4.8 (2.5)	3.6 (1.8)	4.1 (1.8)	4.1 (2.0)	4.1 (1.4)	5.3 (2.1)
SUBSOIL PROPERTIES							
Depth (cm)	40 (33)	57 (40)	59 (28)	39 (22)	30 (19)	71 (28)	50 (31)
Dominant texture class	L	SiL	SiL	SiL	L	SiL	SiL
Clay (%)	19 (3)	27 (14)	22 (7)	20 (5)	25 (9)	22 (8)	21 (6)
Gravel (%)	21 (14)	16 (11)	20 (13)	26 (14)	32 (15)	20 (12)	24 (12)
Total rock (%)	23 (13)	20 (12)	44 (20)	36 (18)	48 (16)	48 (20)	37 (18)
OTHER PROPERTIES							
Depth of fine roots (cm)	32 (12)	37 (15)	30 (14)	40 (15)	38 (17)	36 (11)	45 (16)
Depth where 80% of roots end (cm)	50 (20)	54 (24)	46 (17)	52 (17)	46 (15)	46 (15)	63 (15)
Mollic epipedon depth (cm)	43 (34)	48 (26)	37 (21)	45 (19)	37 (11)	43 (16)	53 (17)
Soil depth (cm)	118 (39)	132 (35)	104 (38)	111 (36)	117 (25)	117 (39)	136 (26)
Total water-holding capacity (cm)	12.7 (5.3)	18.3 (5.6)	10.2 (4.6)	12.2 (5.1)	10.2 (4.1)	10.9 (4.8)	14.7 (5.1)
Slope (%)	20 (21)	16 (13)	24 (16)	17 (14)	33 (18)	26 (16)	28 (15)
Elevation (m)	1818 (83)	1893 (151)	2367 (302)	2142 (232)	2130 (153)	2408 (189)	2147 (171)

Note: Means and standard deviations are the first and (second) entries, respectively.
SL = sandy loam, L = loam, SiL = silt loam, SCL = sandy clay loam, and CL = clay loam.

Heavy clay subsoils (Table 3) limit the soil depth that plants can effectively exploit for available soil moisture on the ARAR C.T.s. The ARNO C.T.s frequently occur on sites with low annual precipitation (i.e., less than 20 cm), which results in a wetting front that probably does not extend throughout the entire soil. Even though deeper soils support ARNO and ARAR C.T.s in this study, the actual depth exploited by plants for soil moisture is probably comparable to that described in Idaho.

Soil temperature and moisture regime relationships for the study area have been described previously (Jensen et al. 1989). Mesic soil temperatures extend to approximately 1,590 m on northern aspects and up to 2,020 m on southern aspects. Cryic soil temperatures are found 81 m and 43 m above these points, respectively. Aridic soil moisture regimes dominate the community types of this study.

The average elevation values presented (Tables 2, 3) suggest that the ARTR/AGSP, ARTR/FEID, ARLO/FEID, ARWY/FEID, and ARNO/ATCO/SIHY C.T.s commonly occur on mesic soils. The ARAR/FEID, ARAR/FEID/POSA, ARNO/AGSP, ARVA/AGSP, ARAR/AGSP, and ARVA/SYOR/AGSP C.T.s occur on cryic soils at higher elevations. Within the ARVA and ARAR C.T.s, *Agropyron spicatum* tends to display dominance over *Festuca idahoensis* as elevation increases.

Festuca idahoensis is commonly used as an indicator of cryic soils in Montana (Mueggler and Stewart 1980, Sasick and Nielson 1984). However, it is not necessarily a good indicator of cryic soils in this study area, because it occurs on mesic, frigid, and cryic soils. Plants most closely associated with cryic soils in this study are *A. tridentata* ssp. *vaseyana* and *Agropyron spicatum*. Their dominance on a site, however, does not always mean that a cryic soil temperature regime is present.

TABLE 3. Comparison of selected average site and soil physical property values by plant community type. *Means underlined by the same line are not significantly different (P < .05) as determined by Duncan's New Multiple Range Test.

A Horizon Clay Content (%)

ARNO ATCO SIHY	ARWY SIHY	ARNO ORHY	ARVA FEID	ARVA AGSP	ARNO AGSP	ARVA SYOR BRCA	ARVA ELCI	ARTR AGSP	ARVA SYOR AGSP	ARAR AGSP	ARTR FEID	ARAR FEID	ARAR FEID POSA	ARLO FEID
15	16	17	17	17	17	17	18	18	18	20	20	20	20	22
———	———	———	———	———	———	———	———	———	———					
							———	———	———	———	———	———	———	———*

Subsoil Clay Content (%)

ARNO ATCO SIHY	ARTR AGSP	ARNO AGSP	ARVA FEID	ARNO ORHY	ARVA SYOR BRCA	ARVA SYOR AGSP	ARVA AGSP	ARWY SIHY	ARVA ELCI	ARTR FEID	ARAR AGSP	ARAR FEID	ARAR FEID POSA	ARLO FEID
18	19	20	20	21	21	22	22	24	25	27	28	30	32	33
———	———	———	———	———	———	———	———	———	———	———				
									———	———	———	———	———	———

Subsoil Total Rock Content (%)

ARTR FEID	ARTR AGSP	ARLO FEID	ARAR FEID	ARVA FEID	ARVA SYOR BRCA	ARWY SIHY	ARNO ATCO SIHY	ARAR FEID POSA	ARNO ORHY	ARAR AGSP	ARVA AGSP	ARNO AGSP	ARVA ELCI	ARVA SYOR AGSP
20	23	30	32	36	37	37	38	39	42	44	44	45	48	48
———	———	———	———											
	———	———	———	———	———	———	———	———	———					
					———	———	———	———	———	———				
						———	———	———	———	———	———	———		
							———	———	———	———	———	———	———	———

Depth Where 80% of the Roots End (cm)

ARLO FEID	ARAR FEID POSA	ARAR FEID	ARNO ORHY	ARAR AGSP	ARWY SIHY	ARNO AGSP	ARNO ATCO SIHY	ARVA ELCI	ARVA AGSP	ARVA SYOR AGSP	ARTR AGSP	ARVA FEID	ARTR FEID	ARVA SYOR BRCA
29	34	35	35	38	28	29	42	46	46	46	50	52	54	63
———	———	———	———	———	———	———	———	———						
								———	———	———	———	———	———	
													———	———

Mollic Epipedon Depth (cm)

ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR FEID POSA	ARAR AGSP	ARWY SIHY	ARAR FEID	ARLO FEID	ARVA ELCI	ARVA AGSP	ARVA SYOR AGSP	ARTR AGSP	ARVA FEID	ARTR FEID	ARVA SYOR BRCA
0	0	16	22	26	27	28	29	37	37	43	43	45	48	53
———	———													
		———	———											
			———	———	———	———	———	———						
					———	———	———	———	———					
							———	———	———	———	———	———	———	
													———	———

Table 3 continued.

Total Soil Depth (cm)

ARAR FEID POSA	ARAR AGSP	ARAR FEID	ARNO ORHY	ARNO AGSP	ARLO FEID	ARNO ATCO SIHY	ARWY SIHY	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARTR AGSP	ARTR FEID	ARVA SYOR BRCA
71	73	74	77	81	81	90	99	104	111	117	117	118	132	136
—	—	—	—	—	—	—	—							
						—	—	—	—	—	—	—		
									—	—	—	—	—	
													—	—

Total Water-Holding Capacity (cm)

ARNO ATCO SIHY	ARNO ORHY	ARAR AGSP	ARWY SIHY	ARAR FEID POSA	ARNO AGSP	ARAR FEID	ARVA ELCI	ARVA AGSP	ARLO FEID	ARVA SYOR AGSP	ARVA FEID	ARTR AGSP	ARVA SYOR BRCA	ARTR FEID
6.3	6.7	7.5	7.7	7.9	8.0	8.4	10.2	10.3	10.7	10.9	12.2	12.8	14.6	18.3
—	—	—	—	—	—	—	—							
						—	—	—	—	—				
									—	—	—	—		
												—	—	
														—

Slope (%)

ARWY SIHY	ARLO FEID	ARAR FEID POSA	ARAR FEID	ARNO ORHY	ARTR FEID	ARVA FEID	ARNO AGSP	ARTR AGSP	ARAR AGSP	ARVA AGSP	ARNO ATCO SIHY	ARVA SYOR AGSP	ARVA SYOR BRCA	ARVA ELCI
4	6	13	13	15	16	17	20	20	24	24	24	26	28	33
—	—	—	—	—	—	—	—							
							—	—	—	—	—	—		
								—	—	—	—	—	—	—

Elevation (m)

ARTR AGSP	ARLO FEID	ARTR FEID	ARWY FEID	ARNO ATCO SIHY	ARAR FEID POSA	ARAR FEID	ARNO ORHY	ARVA ELCI	ARVA FEID	ARVA SYOR BRCA	ARNO AGSP	ARVA AGSP	ARAR AGSP	ARVA SYOR AGSP
1818	1874	1893	1950	1981	2060	2061	2091	2130	2142	2147	2311	2367	2403	2408
—	—	—	—	—	—	—								
	—	—	—	—	—	—	—	—	—	—				
											—	—	—	—

Significant differences in ground cover exist between community types (Tables 4, 5). Average vegetation and litter ground cover are both significantly higher on ARTR and ARVA C.T.s than on ARNO C.T.s. Conversely, average gravel ground cover is significantly higher on ARNO C.T.s. In a study of southern Idaho sagebrush communities, Jensen (1983) found soil erosion loss to be negatively correlated with vegetation and litter, and positively correlated with bare ground and gravel cover. These relationships suggest that C.T.s with *A. nova*, *A. arbuscula*, and *A. longiloba* as the dominant sagebrush species experience higher soil erosion losses than do *A. tridentata*–dominated C.T.s. Observations of soil

TABLE 4. Relative percentage of total ground cover contributed by various components by sagebrush community type.

Ground cover component		Community type														
		ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWY SIHY	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
		n = 12	n = 16	n = 44	n = 27	n = 19	n = 19	n = 4	n = 4	n = 6	n = 8	n = 63	n = 67	n = 9	n = 23	n = 47
% Veg + Litter	($\bar{X}$)	36	39	44	50	52	60	58	72	71	82	59	78	64	63	78
	(S)	13	11	14	12	15	15	14	12	18	14	17	14	19	14	14
	(SE)	4	3	2	2	4	3	7	6	7	5	2	2	6	3	2
% Bare soil	($\bar{X}$)	22	24	15	10	15	14	23	19	22	15	13	12	24	21	14
	(S)	12	10	8	6	10	10	16	2	14	10	10	8	18	7	11
	(SE)	3	3	1	1	2	2	8	1	6	4	1	1	6	1	2
% Gravel	($\bar{X}$)	34	33	36	31	26	21	18	8	4	3	21	8	7	12	7
	(S)	7	13	15	15	16	17	18	9	5	5	14	11	8	11	10
	(SE)	2	3	2	3	4	4	9	4	2	2	2	1	3	2	2
% Cobble + stone	($\bar{X}$)	9	4	4	9	5	1	2	1	3	1	7	1	4	4	1
	(S)	10	6	5	8	6	2	2	2	4	1	8	2	6	6	2
	(SE)	3	1	1	2	1	1	1	1	2	1	1	1	2	1	1

Note: $\bar{X}$ = mean, S = standard deviation, SE = standard error.

erosion indicators (e.g., rilling, surface soil displacement) made over the sample sites support this assumption.

Soil Chemical Property Relationships

Limited soil chemical data exist for Great Basin rangelands. The surface (Tables 6, 8) and subsoil (Table 7) soil chemical values recorded for the community types of this study provide needed baseline data for relatively undisturbed rangeland communities.

Soil salinity was low in all the community types studied with the exception of the ARNO/ATCO/SIHY C.T., which has high average salinity (i.e., 2.8 deci-Siemen per meter [d S/m]) in its subsoils (Table 7). Such values are comparable to those recorded in other *Atriplex* communities (Sharma 1973, Sharma and Tongway 1973). The ARNO/ATCO/SIHY C.T. in this study is limited to sites with relatively high soluble salt concentrations. None of the soils studied are adversely affected by sodium; however, the ARLO/FEID C.T. has an average subsoil exchangeable sodium percentage (ESP) of 15%, which is much higher than any other C.T. It appears that this community type is best adapted to sites with both high clay and high sodium contents in the subsoil.

Soil calcium carbonate content tends to be very high at sites dominated by *A. nova* (e.g., ARNO/ORHY, ARNO/AGSP C.T.s) and is low at sites dominated by *A. arbuscula* (e.g., ARAR/FEID, ARAR/FEID/POSA). These two sagebrush species commonly grow in contiguous populations in the study area and often occur on similar topographic and climatic environments. Their distribution under such situations is correlated with the abundance of free carbonates in the soils that support them. *Artemisia nova* occupies sites with abundant carbonates (e.g., limestone parent materials), and *A. arbuscula* is restricted to sites without abundant carbonates (e.g., granitic parent materials). Within a given C.T. series (e.g., ARVA), *Agropyron spicatum* is the dominant graminoid on sites with abundant carbonates, and *Festuca idahoensis* is dominant when the soil does not contain free carbonates. These relationships have also been suggested for southern Idaho rangelands (Hironaka et al. 1983).

Exchangeable calcium within the surface soil shows significant differences between C.T.s (Table 8). ARWY and ARNO C.T.s have significantly more exchangeable calcium in their surface soils than ARTR, ARVA, and ARAR C.T.s. This same relationship was also observed for subsoil calcium levels.

Surface soil pH follows a similar trend, with ARNO and ARWY C.T.s displaying significantly higher values than other C.T.s. Graminoid species such as *Oryzopsis hymenoides* (ORHY) and *Sitanion hystrix* (SIHY) dominate the understory layer of a C.T. when surface pH values are moderately alkaline, *Agropyron spicatum* dominates when pH values

TABLE 5. Comparison of selected average ground cover component values by plant community type. *Means underlined by the same line are not significantly different ($P < .05$) as determined by Duncan's New Multiple Range Test.

Vegetation and Litter Ground Cover (%)

ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARLO FEID	ARVA AGSP	ARAR FEID	ARVA SYOR AGSP	ARVA ELCI	ARTR AGSP	ARWY SIHY	ARVA SYOR BRCA	ARVA FEID	ARTR FEID
36	39	44	50	52	58	59	60	63	64	71	73	78	78	82
―	―	―												
		―	―	―	―									
				―	―	―	―							
						―	―	―	―	―	―			
										―	―	―	―	― *

Bare Soil Ground Cover (%)

ARAR AGSP	ARVA FEID	ARVA AGSP	ARVA SYOR BRCA	ARAR FEID	ARNO AGSP	ARAR FEID POSA	ARTR FEID	ARWY SIHY	ARVA SYOR AGSP	ARNO ATCO SIHY	ARTR AGSP	ARLO FEID	ARNO ORHY	ARVA ELCI
10	12	13	14	14	15	15	15	19	21	22	22	23	24	24
―	―	―	―	―	―	―	―	―						
						―	―	―	―	―	―	―	―	
									―	―	―	―	―	―

Gravel Ground Cover (%)

ARTR FEID	ARTR AGSP	ARVA ELCI	ARVA SYOR BRCA	ARWY SIHY	ARVA FEID	ARVA SYOR AGSP	ARLO FEID	ARAR FEID	ARVA AGSP	ARAR FEID POSA	ARAR AGSP	ARNO ORHY	ARNO ATCO SIHY	ARNO AGSP
3	4	7	7	8	8	12	18	21	21	26	31	33	34	36
―	―	―	―	―	―	―	―							
							―	―	―	―				
										―	―	―	―	
												―	―	―

are neutral, and *Festuca idahoensis* dominates when pH values are moderately acid. Observation of soil properties associated with common grass species of the Great Basin by Platou et al. (1986) supports the pH relationships observed in this study.

Surface soil organic matter and nitrogen contents (Table 8) display differences between C.T.s. The ARNO, ARWY, and ARLO C.T.s have significantly lower nitrogen contents than ARVA C.T.s. This same trend is also present for organic matter, with the exception of the ARNO/AGSP C.T., which has organic matter contents similar to those found in ARVA C.T.s. In a study of habitat differences between *A. tridentata* ssp. *tridentata* and *wyomingensis* in Utah, Barker and McKell (1983) found that *A. tridentata* ssp. *tridentata* occupied more fertile environments. Those authors showed that soils supporting *A. tridentata* ssp. *tridentata* always have higher levels of organic carbon, nitrogen, and phosphorus than those supporting *A. tridentata* ssp. *wyomingensis*. These same relationships exist in this study area, with ARTR/FEID and ARTR/AGSP C.T. soils displaying higher average values for these elements than soils of the ARWY/SIHY C.T.

CONCLUSION

Soil physical and chemical properties were studied to identify habitat differences among sagebrush-dominated plant communities of

TABLE 6. Surface (0–15 cm) soil chemical property values by sagebrush community type.

	Community type							
Property	ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWY SIHY
	n = 11	n = 13	n = 36	n = 24	n = 18	n = 19	n = 4	n = 4
pH	7.8 (0.5)	7.5 (0.4)	7.8 (0.5)	7.0 (0.4)	6.6 (0.4)	6.4 (0.3)	6.4 (0.2)	7.7 (0.5)
CEC (meq/100 g)	20.1 (3.9)	22.2 (7.2)	22.7 (5.4)	19.7 (6.4)	20.4 (6.9)	21.2 (4.6)	19.7 (2.3)	21.0 (6.7)
Organic matter (%)	2.0 (0.8)	2.5 (1.2)	4.3 (1.7)	4.1 (1.9)	3.8 (2.2)	3.7 (1.4)	3.6 (2.2)	2.2 (0.6)
Total N (%)	0.06 (0.02)	0.07 (0.02)	0.12 (0.06)	0.14 (0.10)	0.12 (0.08)	0.17 (0.06)	0.11 (0.04)	0.11 (0.08)
C/N ratio	20 (10)	20 (11)	24 (16)	21 (12)	29 (24)	15 (10)	22 (11)	18 (10)
Na (meq/100 g)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)
K (meq/100 g)	0.8 (0.4)	0.7 (0.5)	0.9 (0.5)	1.4 (1.9)	0.9 (0.9)	1.0 (0.5)	1.4 (1.9)	1.6 (1.0)
Ca (meq/100 g)	16.9 (4.2)	18.1 (9.5)	19.0 (7.1)	13.7 (5.4)	12.5 (4.5)	12.1 (2.1)	10.4 (1.1)	21.0 (10.5)
Mg (meq/100 g)	2.6 (1.2)	4.6 (3.8)	4.0 (3.6)	3.7 (1.9)	5.0 (2.8)	3.4 (0.8)	4.9 (3.3)	7.6 (5.8)
Zn (ppm)	---	---	4.0 (1.0)	1.6 (0.6)	2.0 (1.7)	1.7 (0.9)	1.0 (0.5)	1.0 (0.5)
P (ppm)	9.2 (4.5)	10.5 (6.5)	7.6 (4.2)	9.7 (3.9)	9.1 (5.1)	12.2 (8.3)	12.5 (6.1)	15.2 (17.3)
Calcium carbonate equivalent (%)	10.1 (7.5)	17.8 (15.3)	18.7 (13.2)	2.6 (3.0)	1.1 (1.5)	0.1 (0.5)	1.0 (0.2)	5.7 (5.2)
Electrical conductivity (dS/m)*	0.4 (0.2)	0.3 (0.2)	0.4 (0.1)	0.4 (0.3)	0.4 (0.5)	0.9 (0.5)	1.8 (0.4)	0.4 (0.2)
Base saturation (%)	100 (0)	97 (4)	95 (16)	93 (10)	87 (12)	82 (9)	77 (10)	100 (0)

TABLE 6 continued.

	Community type						
Property	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
	n = 6	n = 8	n = 54	n = 61	n = 7	n = 23	n = 43
pH	7.0 (0.9)	6.4 (0.5)	7.0 (0.6)	6.2 (0.4)	6.4 (0.4)	7.0 (0.7)	6.4 (0.4)
CEC (meq/100 g)	19.7 (5.1)	22.5 (5.0)	20.4 (5.1)	22.6 (5.4)	20.4 (7.2)	21.9 (5.3)	23.5 (4.6)
Organic matter (%)	2.6 (1.3)	4.8 (1.2)	4.6 (2.0)	4.5 (1.8)	3.9 (2.5)	5.5 (2.2)	5.0 (1.7)
Total N (%)	0.14 (0.08)	0.21 (0.08)	0.16 (0.07)	0.22 (0.07)	0.22 (0.07)	0.19 (0.07)	0.27 (0.12)
C/N ratio	11 (1)	16 (9)	19 (10)	14 (7)	11 (6)	21 (11)	13 (8)
Na (meq/100 g)	0.1 (0)	0.1 (0)	0.1 (0)	0.1 (0)	0.1 (0)	0.1 (0)	0.1 (0)
K (meq/100 g)	1.2 (0.5)	1.3 (0.6)	1.0 (1.0)	1.2 (0.4)	1.2 (0.5)	1.3 (1.0)	1.2 (0.6)
Ca (meq/100 g)	12.9 (4.7)	11.6 (2.4)	13.9 (5.3)	11.5 (3.5)	10.6 (2.9)	14.9 (5.2)	12.8 (3.5)
Mg (meq/100 g)	3.2 (1.3)	3.2 (1.1)	3.5 (2.8)	3.6 (2.4)	4.3 (3.5)	3.1 (2.4)	3.4 (2.2)
Zn (ppm)	2.2 (1.2)	4.4 (1.6)	3.5 (3.6)	3.3 (2.5)	6.7 (3.3)	4.4 (3.7)	8.7 (6.6)
P (ppm)	17.2 (13.2)	26.1 (13.9)	13.7 (9.2)	14.1 (8.6)	31.8 (14.0)	14.5 (9.2)	25.2 (15.7)
Calcium carbonate equivalent (%)	0.8 (1.0)	0.5 (1.2)	7.0 (10.1)	0.1 (0.5)	0.1 (0.4)	5.4 (7.1)	0.1 (0.4)
Electrical conductivity (dS/m)	0.3 (0.1)	0.5 (0.4)	0.4 (0.2)	0.6 (0.6)	0.4 (0.2)	0.5 (0.4)	0.2 (0.1)
Base saturation (%)	88 (13)	75 (11)	88 (15)	74 (13)	76 (16)	87 (12)	76 (10)

Note: Values provided correspond to mean and (standard deviation), respectively.
*dS/M = deci-Siemen per meter.

the Great Basin region. Significant differences in soil properties exist between certain community types, and thus support the use of vegetation classification systems in defining ecosystems (Hironaka et al. 1983). Soil properties do exhibit large variability within certain community types (e.g., those dominated by *A. tridentata* ssp. *vaseyana*). This variability suggests that caution be employed when inferring soil relationships based solely upon the plant community expression present at a site. Data from this study provide baseline information concerning soil relationships within relatively undisturbed rangeland communities. Such data are required if future soil sampling efforts within the Great Basin are to have a basis for comparison.

TABLE 7. Subsoil (40–60 cm) soil chemical property values by sagebrush community type.

	Community type							
Property	ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWY SIHY
	n = 11	n = 13	n = 36	n = 24	n = 18	n = 19	n = 4	n = 4
pH	7.8 (0.3)	7.7 (0.4)	8.0 (0.4)	7.5 (0.5)	6.6 (0.6)	6.3 (0.6)	6.4 (0.7)	7.2 (0.5)
CEC (meq/100 g)	28.0 (7.3)	25.3 (4.2)	24.0 (3.8)	24.9 (9.0)	27.5 (10.6)	24.0 (10.2)	21.7 (5.0)	25.0 (7.5)
Organic matter (%)	1.4 (0.6)	2.5 (1.1)	2.5 (0.9)	1.8 (0.8)	1.8 (0.8)	1.5 (1.1)	1.9 (1.4)	2.1 (1.4)
Na (meq/100 g)	0.2 (0.1)	0.2 (0.2)	0.2 (0.2)	2.1 (2.0)	0.3 (0.2)	0.3 (0.6)	3.3 (2.0)	0.1 (0.1)
K (meq/100 g)	0.7 (0.4)	0.8 (0.7)	0.5 (0.3)	0.9 (1.9)	0.8 (0.6)	0.8 (0.6)	1.6 (2.1)	1.5 (1.6)
Ca (meq/100 g)	14.2 (6.2)	15.7 (9.2)	14.4 (5.8)	14.5 (6.5)	16.1 (7.7)	14.4 (7.0)	12.6 (3.2)	24.2 (13.0)
Mg (meq/100 g)	8.4 (3.1)	8.1 (3.4)	6.9 (3.7)	7.0 (3.4)	7.0 (2.8)	5.6 (2.7)	5.0 (3.6)	8.7 (5.7)
Zn (ppm)	---	---	1.0 (1.0)	1.0 (0)	1.0 (0)	1.0 (0)	1.0 (0)	1.0 (1.0)
P (ppm)	2.8 (1.0)	5.2 (3.4)	3.8 (2.0)	4.6 (3.9)	4.7 (2.8)	6.8 (4.0)	3.7 (0.5)	4.3 (2.5)
Calcium carbonate Equivalent (%)	6.4 (6.3)	23.4 (21.2)	24.1 (18.2)	3.7 (6.1)	1.8 (1.3)	0 (0)	0 (0)	5.0 (4.2)
Electrical conductivity (dS/m)*	2.8 (4.6)	0.4 (0.1)	0.4 (0.2)	0.9 (1.0)	0.6 (0.9)	0.3 (0.1)	0.2 (0)	0.4 (0.1)
Base saturation (%)	100 (0)	100 (0)	100 (0)	100 (0)	89 (10)	88 (9)	86 (4)	97 (1)

TABLE 7 continued.

	Community type						
Property	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
	n = 6	n = 8	n = 54	n = 61	n = 7	n = 23	n = 43
pH	6.6 (1.5)	6.2 (0.2)	7.4 (0.8)	6.3 (0.5)	6.6 (0.7)	7.2 (0.8)	6.5 (0.5)
CEC (meq/100 g)	19.7 (8.0)	22.1 (6.8)	19.7 (4.9)	19.8 (7.2)	20.0 (7.3)	21.4 (6.0)	20.0 (5.2)
Organic matter (%)	2.0 (0.7)	2.3 (1.0)	2.2 (0.9)	2.3 (1.0)	2.5 (0.7)	3.1 (1.2)	3.1 (1.3)
Na (meq/100 g)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)
K (meq/100 g)	1.1 (0.5)	1.0 (0.6)	0.8 (0.6)	1.0 (0.5)	0.9 (0.5)	1.1 (1.2)	1.0 (0.4)
Ca (meq/100 g)	11.8 4.0)	12.3 (4.1)	12.5 (4.5)	10.6 (4.9)	11.2 (3.3)	15.0 (6.4)	11.5 (3.8)
Mg (meq/100 g)	6.9 (3.4)	5.8 (4.0)	7.2 (7.2)	4.0 (2.9)	3.9 (3.1)	8.1 (19.8)	3.9 (3.0)
Zn (ppm)	1.0 (1.0)	2.0 (1.0)	2.7 (3.4)	1.1 (0.6)	2.4 (1.5)	1.7 (1.2)	3.8 (4.8)
P (ppm)	10.3 (3.8)	17.8 (14.7)	10.1 (12.4)	10.0 (9.6)	17.8 (6.1)	7.7 (8.1)	11.0 (7.1)
Calcium carbonate Equivalent (%)	0.7 (1.1)	0 (0)	5.6 (8.3)	0.2 (1.0)	0.3 (0.7)	7.4 (8.5)	0.3 (1.0)
Electrical conductivity (dS/m)	0.5 (0.4)	0.2 (0.1)	0.6 (0.6)	0.2 (0.1)	0.2 (0.1)	1.0 (1.4)	0.1 (0.1)
Base saturation (%)	79 (29)	78 (8)	94 (8)	74 (15)	80 (20)	92 (11)	78 (11)

Note: Values provided correspond to mean and (standard deviation), respectively.
*dS/m = deci-Siemen per meter.

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TABLE 8. Comparison of selected average soil surface (0–15 cm) chemical property values by plant community type. *Means underlined by the same line are not significantly different ($P < .05$) as determined by Duncan's Multiple Range Test.

pH

ARNO ATCO SIHY	ARNO AGSP	ARWY SIHY	ARNO ORHY	ARAR AGSP	ARVA AGSP	ARTR AGSP	ARVA SYOR AGSP	ARAR FEID POSA	ARLO FEID	ARVA ELCI	ARAR FEID	ARVA SYOR BRCA	ARTR FEID	ARVA FEID
7.8	7.8	7.7	7.5	7.0	7.0	7.0	7.0	6.6	6.4	6.4	6.4	6.4	6.2	6.2
———	———	———	———											
				———	———	———	———							
								———	———	———	———	———	———	——— *

Organic Matter (%)

ARNO ATCO SIHY	ARWY SIHY	ARTR AGSP	ARNO ORHY	ARLO FEID	ARAR FEID	ARAR FEID POSA	ARVA ELCI	ARAR AGSP	ARNO AGSP	ARVA FEID	ARVA AGSP	ARTR FEID	ARVA SYOR BRCA	ARVA SYOR AGSP
2.0	2.2	2.6	2.6	3.7	3.7	3.8	4.0	4.1	4.3	4.5	4.6	4.8	5.0	5.5
———	———	———	———	———										
	———	———	———	———	———	———	———							
					———	———	———	———	———	———	———	———		
										———	———	———	———	———

Total Nitrogen (%)

ARNO ATCO SIHY	ARNO ORHY	ARWY SIHY	ARLO FEID	ARAR FEID POSA	ARNO AGSP	ARTR AGSP	ARAR AGSP	ARVA AGSP	ARAR FEID	ARVA SYOR AGSP	ARTR FEID	ARVA ELCI	ARVA FEID	ARVA SYOR BRCA
0.06	0.07	0.11	0.11	0.12	0.13	0.14	0.14	0.16	0.17	0.19	0.21	0.22	0.22	0.27
———	———	———	———	———										
	———	———	———	———	———	———								
		———	———	———	———	———	———	———	———					
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TABLE 8 continued.

Exchangeable Calcium (meq/100 g)

ARLO FEID	ARVA ELCI	ARVA FEID	ARTR FEID	ARAR FEID	ARAR FEID POSA	ARVA SYOR BRCA	ARTR AGSP	ARAR AGSP	ARVA AGSP	ARVA SYOR AGSP	ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARWY SIHY
10.4	10.6	11.5	11.6	12.1	12.5	12.8	12.9	13.7	13.9	14.9	16.9	18.1	19.0	21.0
—	—	—	—	—	—	—	—	—	—					
								—	—	—	—			
											—	—		
												—	—	—

Available Phosphorus (ppm)

ARNO AGSP	ARAR FEID POSA	ARNO ATCO SIHY	ARAR AGSP	ARNO ORHY	ARAR FEID	ARLO FEID	ARVA AGSP	ARVA FEID	ARVA SYOR AGSP	ARWY SIHY	ARTR AGSP	ARVA SYOR BRCA	ARTR FEID	ARVA ELCI
7.6	9.1	9.2	9.7	10.5	12.2	12.5	13.7	14.1	14.5	15.2	17.2	25.2	26.1	31.8
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HYOBRANCHIAL APPARATUS OF THE CRYPTOBRANCHOIDEA (AMPHIBIA)

Douglas C. Cox[1] and Wilmer W. Tanner[1]

ABSTRACT.—This report is a comparative study of the hyobranchial skeleton of the three species in the family Cryptobranchidae and four species of the family Hynobiidae, all of which are figured. Anatomical differences between the cryptobranchids and their relationship to hynobiids are noted and discussed. Reference is made to a relationship that may exist between these families and other salamander families, particularly the possible relationship of the Hynobiidae to the super families Ambystomatoidea or possibly Plethodontoidea.

The primary purpose of this study was to examine and compare the hyobranchial skeleton of representatives of the families Cryptobranchidae and Hynobiidae. We were concerned not only with the anatomical relationships of the two families, but also with the basic differences between available genera within the families. Much has been done to establish an understanding of anatomical relationships primarily involving skeletal and soft tissue comparative anatomy of other families, particularly Ambystomatidae, Plethodontidae, and Salamandridae. The studies by Humphry (1872) and Dunn (1923, 1926) were followed by research of Noble (1931), Francis (1934), Edgeworth (1935), Piatt (1935, 1939, 1940), Taylor (1944), Tanner (1950, 1952), Fox (1954), Wake (1966), Wake and Ozeti (1969), Nickerson and Mays (1972), Estes (1981), Duellman and Trueb (1986), and others cited below, involving cytogenetic studies with the intent to provide data showing familial relationships.

The examination of the relationships of the Cryptobranchoidea by Dunn (1923) established the primitive characters of external fertilization and retention of the angular bone in the lower jaw. These characters have not only placed the cryptobranchids and hynobiids as primitive groups of salamanders, but also as possible descendants of ancestral stock similar to those from which other salamander lines might have arisen. Dunn (1923) also noted the following: both families possess nasals that meet at the middorsal line, and the premaxillary spines are short in contrast to other families with separate nasals and long spines.

Recent studies also indicate that the cryptobranchids are primitive in that they have a large number of chromosomes (60). Morescalchi et al. (1977, 1979) give the structure and numbers of chromosomes for the three cryptobranchid species, with each having 60, and list the following hynobiid species and their chromosome numbers: *Ranodon sibiricus*, 2n = 66; *Batrachuperus mustersi*, 2n = 62; *Onychodactylus japonicus*, 2n = 58 ± 2; *Hynobius dunni*, *H. nebulosus*, and *H. tsuensis*, each with 2n = 56. A study by Sessions et al. (1982) provides essentially the same information, listing 30 pairs of chromosomes in the genus *Andrias* as compared to 11–14 pairs in other families of North American salamanders. Taketa and Nickerson (1973) determined the relative electrophoretic mobilities of the hemoglobins of three families of salamanders represented by *Cryptobranchus*, *Necturus*, and *Hynobius*, when compared with adult human HbA, at pH 8.4. It is noteworthy that *Cryptobranchus* has a single component with greater mobility than the two components in *Hynobius tsuensis*.

The relationship of the cryptobranchids to other families of salamanders and particularly to the hynobiids was noted by Dunn (1923). He indicated that cryptobranchids are more closely related to the hynobiids than perhaps to other salamander families. While this may yet be true, there are substantial differences between the basic structures of the throat anatomy of the hynobiids and the cryptobranchids. This is particularly evident in the bony and cartilaginous structures. If there is indeed a close relationship, it is apparently one based on such characters as external fertilization, retention of the angular bone, and greater number of chromosomes, and not on the hyobranchial structures, which have undergone major modifications that would suggest not only an extended period of isolation, but certainly one in which major adaptive modifications have occurred. Furthermore, there has been a major radiation in the family Hynobiidae that has not occurred among the cryptobranchids.

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The fossil history of the development of the various families of salamanders indicates that there may have been a movement of representatives of two major families from North America into the Orient. Certainly North America has been a center for major salamander evolution, with all families (except Hynobiidae) being represented. Only four of the seven families have extended their distributions beyond the North American shores (Plethodontidae—Europe; Ambystomatidae, Cryptobranchidae, and Hynobiidae—Asia). The families Ambystomatidae and Cryptobranchidae are represented on both the Asiatic and American continents, with the Asiatic cryptobranchids having developed giantism and undergone a more complete morphological development than the American representatives.

The place of origin for the Cryptobranchoidea and particularly the family Cryptobranchidae is as yet uncertain. Meszoely (1967) described as new the genus *Piceoerpeton* from fossil vertebrae obtained from the early Eocene of Wyoming and included it in the family Cryptobranchidae. Within the family it is related to the genus *Andrias*. Estes (1969) maintained that the relationship of the genus *Piceoerpeton* is better placed in the family *Scapherpetontidae*, a representative of Ambystomatoidea. The occurrence of *Andrias* in Europe and Japan (Westphal 1958) suggests a previously wide distribution for the family and perhaps for the genus *Andrias* in North America, although this has not as yet been demonstrated.

An examination of the throat skeleton suggests that *Andrias* has advanced beyond the semilarval condition seen in *Cryptobranchus* with its retained gill bars (Figs. 1–3). The two oriental species (*A. davidianus* and *M. japonicus*) have a greater similarity in hyobranchial structures than either has with adult *C. alleganiensis*, and both are much larger.

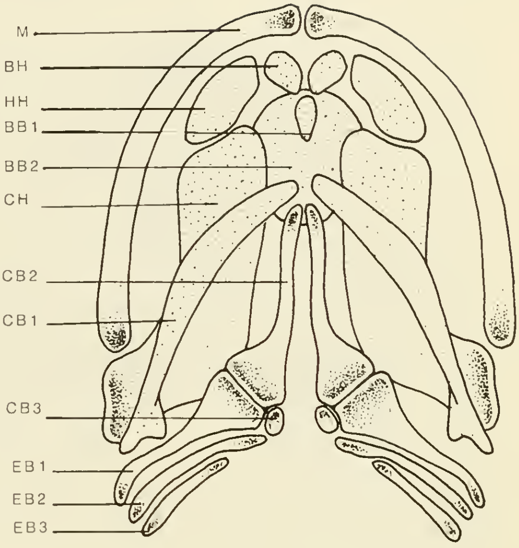

Fig. 1. Ventral view of the hyobranchial apparatus of *Cryptobranchus alleganiensis*. M = lower jaw; BH = basihyal; HH = hypohyal; BB1 = basibranchial #1; BB2 = basibranchial #2; CH = ceratohyal; CB1 = ceratobranchial #1; CB2 = ceratobranchial #2; EB1 = epibranchial #1; BB3 = basibranchial #3; EB2 = epibranchial #2; EB3 = epibranchial #3.

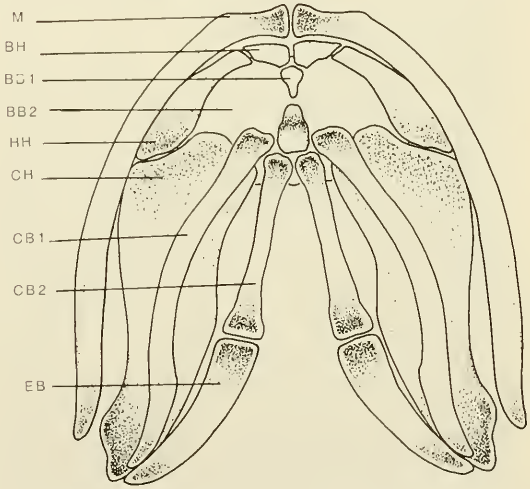

Fig. 2. Ventral view of the hyobranchial apparatus of *Megalobatrachus japonicus*.

A comparison of the hyobranchial skeleton of Hynobiidae to that of Cryptobranchidae indicates major differences not only in the position of basic structures but also in relative size and shape (Fig. 4). If these families are retained in the same superfamily (Cryptobranchoidea), their retention must be based

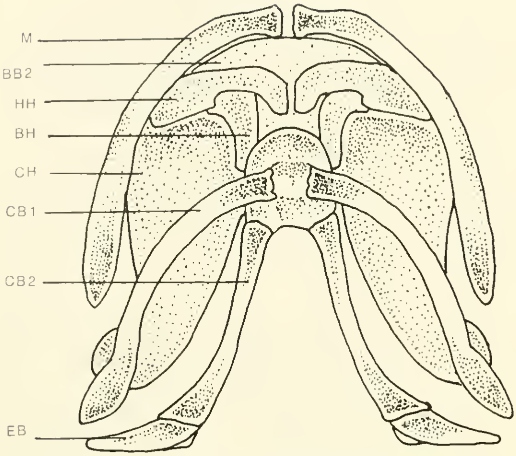

Fig. 3. Ventral view of the hyobranchial apparatus of *Andrias davidianus*.

on the primitive characters indicated above and not on the skeletal characters of the throat.

The following is a description of the structures of the hyobranchial apparatus as observed in some members of the superfamily Cryptobranchoidea.

The hyobranchial apparatus of the family Cryptobranchidae consists of cartilaginous and bony elements. It has the following features: basibranchials, ceratohyals, hypohyals, basihyals, ceratobranchials, and epibranchials. The first basibranchial is a small cartilage located in the anterior median area of the throat. It is loosely joined to the basihyals and is ventral to the enlarged second basibranchial. It was observed in all dissections except *Andrias davidianus*. The second basibranchial is larger than the first and is platelike in all. It provides broad support for the floor of the mouth, joins with the first and second ceratobranchials and in the Asian species includes a distinct ventral process that makes a strong joint with the ceratobranchials. This cartilage is largest in the Asian species, filling the anterior third of the space between the rami of the mandibles. The basihyals, hypohyals, and ceratohyals form a cartilaginous arch that follows the contour of the jaw. There does not appear to be any hard tissue connection between the elements of this arch and other hyobranchial structures. *Andrias davidianus* differs from all others in the arrangement of the basihyals and the hypohyals. The hypohyals are enlarged and curved, meeting at the midventral line and also forming a broad joint with the ceratohyals. The basihyals have been pushed caudad and lie on the medial border of the ceratohyals and the posterior border of the hypohyal. There is some doubt as to the proper names to be applied to these cartilages; a final determination may require a careful examination of the embryonic development of these structures in this species.

An examination of the position of the hyobranchial apparatus in the two families (Figs. 1–4) indicates a noticeable posterior shift of all structures in the family Hynobiidae. This has raised a question as to whether the structure we have labeled the first basibranchial in Figures 1 and 2 is a basibranchial or a separate segment of the first arch. In any case it is not possible to relate these structures (basibranchials) to homologous structures in hynobiids using only adult specimens.

The structure of the hyobranchial apparatus has been illustrated as we found it to occur in the dissections of *Andrias davidianus*, *Megalobatrachus japonicus*, and *Cryptobranchus alleganiensis* (Figs. 1–3). The semilarval condition of the American hellbender (*C. alleganiensis*) is evident by the presence of gill bars, which are ossified, and by the remaining gill slit (Fig. 3). These structures were found in both *C. a. alleganiensis* and *C. a. bishopi*. No such structures were found in the Asian species. Both ceratobranchials were ossified in the Asian forms, but in *Cryptobranchus* only the second ceratobranchial shows evidence of ossification. The cartilage components of *Cryptobranchus* are rounded and tend to be loosely joined; this condition also suggests the immature status of the American species.

The hyobranchial apparatus of *Hynobiidae* was determined by dissection of four species: *Hynobius naevius*, *H. keyserlingii*, *H. tsuensis*, and *Ranodon sibiricus*. The hynobiid salamanders show remarkable conformity to a specific morphologic pattern that is unlike that found in any other salamander group. The curious structure of the ceratohyals is an example (Fig. 4). The evolutionary pressures must have been strong, as similarities to their supposed nearest relatives, the cryptobranchids, are few.

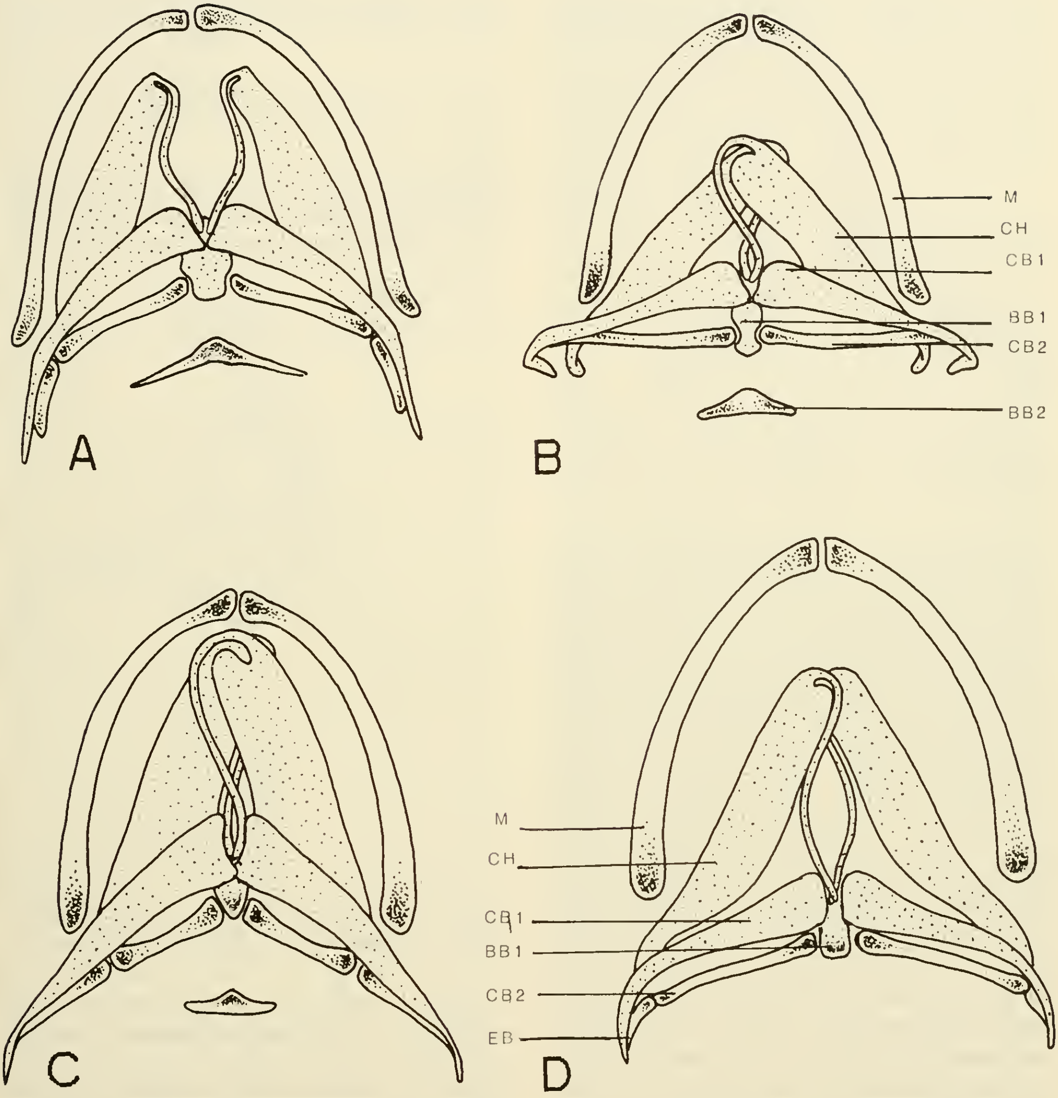

Fig. 4. Ventral view of the hyobranchial apparatus of: A, *Ranodon sibericus;* B, *Hynobius keyserlingii;* C, *Hynobius naevius;* and D, *Hynobius tsuensis.* M = lower jaw; CH = ceratohyal; CB1 = ceratobranchial #1; BB1 = basibranchial #1; CB2 = ceratobranchial #2; BB2 = basibranchial #2; EB = epibranchial.

The hynobiid salamanders possess the following structures as part of the hyobranchial apparatus: first and second basibranchial, ceratohyal, ceratobranchial, and epibranchial. The first basibranchial is small and rodlike, with small anterolateral cornua (Fig. 5). The first and second ceratobranchials attach solidly to the first basibranchial. There does not appear to be any direct attachment with the ceratohyals. The basihyals and the hypohyals are missing or perhaps fused with the ceratohyals. The ceratohyals are broad, flat, and thin cartilages that lie lateral and anterior to other parts of the hyobranchial apparatus. The anterior end of the ceratohyal is located near the symphysis of the lower jaw. A curious extension of the lateral edge of the ceratohyal is drawn out into a small rod that loops over the anterior end of the cartilage and continues posteriorly along the medial line, ending in

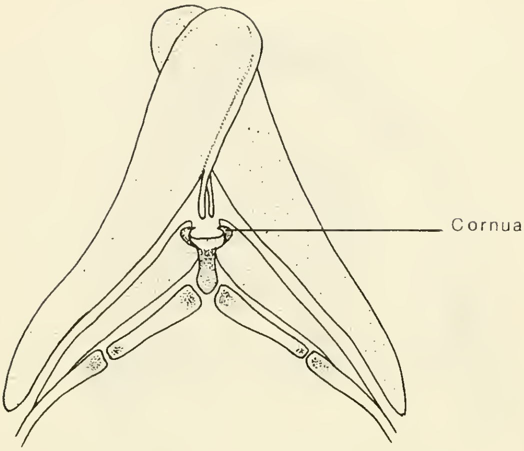

Fig. 5. Dorsal view of the hyobranchial apparatus of *Hynobius naevius*.

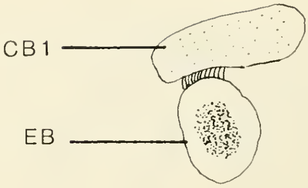

Fig. 6. Cross section of the distal ends of the ceratobranchial and epibranchial as observed in Hynobiidae. CB1 = ceratobranchial #1; EB = epibranchial.

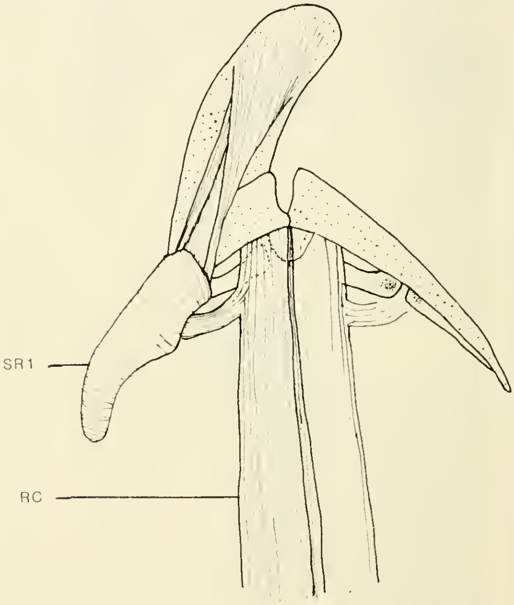

Fig. 7. Musculature of the ceratobranchial complex. SR1 = Subarcualis rectus 1; RC = Rectus cervicis.

connective tissue and bound with its partner, just dorsal to and at the anterior end of the basibranchial (Fig. 5). The first ceratobranchial is also flattened and relatively large, with its anterior end located at the level of the anterior end of the basibranchial and connected to its ventral surface. The ceratobranchial is found ventral to and overlapping the posterior half of the ceratohyal. The posterior portion of the second ceratobranchial and its epibranchial are closely adherent to a flattened distal surface of the first ceratobranchial. These are tightly bound together by connective tissue and muscle fibers (Figs. 6, 7). We did not find an epibranchial on the first ceratobranchial. The second ceratobranchial is small and rodlike. It is attached at its anterior end to the posterior end of the first basibranchial and extends posterolaterally, to be partially encased with the first ceratobranchial. The unity of the first and second ceratobranchials is further evidenced by the presence of the subarcualis rectus 1 muscle. This muscle originates on the anterior ventral surface of the ceratohyal and extends posteriorly to wrap and encase the lateral ends of the first and second ceratobranchials (Fig. 7). A slip of the rectus cervicis muscle also extends laterally to become incorporated into this same structure. This same muscle arrangement also occurs in primitive plethodontid salamanders and operates the functions of the tongue. In the more advanced plethodontid salamanders the tongue is free and the subarcualis rectus 1, by its contraction, is able to extend the tongue a great distance out of the mouth in order to capture prey. The more primitive plethodontids, lacking the free tongue, are closer to the condition observed in the hynobiids. Dunn (1923) referred to the hynobiid tongue as being "sessile, but free at the lateral and posterior edges." The argument by Regal (1966) that there is a relationship between the feeding patterns (and perhaps a relationship in the anatomical structures associated with feeding) of Ambystomatidae, Plethodontidae, and Hynobiidae may warrant more consideration than it has received.

Three of the four species dissected possess a second basibranchial (os thyroidum) (Figs. 4A,B,C), a small triangular bone found posterior to the other structures of the hyobranchial apparatus. This small bone is connected to the hyobranchial apparatus by connective tissue and muscle fibers. It was not found in *H. tsuensis*.

The dissections of the four species of the family Hynobiidae demonstrate a remarkably uniform consistency in the structures of the hyobranchial apparatus. This is especially true when we consider that the family has undergone an adaptive radiation that has resulted in systematists dividing the family into nine genera (Duellman and Trueb 1986). There is also remarkable variation between hynobiid throat structures and those of other families.

Two characters appear to be unique to the family Hynobiidae. The anterior end of the ceratohyl thins into a slender rod of cartilage that extends mesally and ventrally to approach or contact the anterior end of the first basibranchial. The posterior ends of the ceratobranchial rods are encased in connective tissue and are not solidly attached to the basibranchial; thus, it appears that considerable flexibility of movement occurs. This latter may be ascertained from the position of these structures as drawn from the preserved specimens.

The distal third of the first ceratobranchial has a flattened surface on its mesal side onto which the posterior part of the second ceratobranchial and its epibranchial are tightly enclosed by connective and muscle tissues (Fig. 6). This may provide greater support in the center of the throat area. This structure is reminiscent of the M. subarcualis rectus that occurs in some plethodontids, the genus *Pseudoeurycea*, as an example (Tanner 1952). The presence of the second basibranchial in essentially the same location as in primitive plethodons is also suggestive of an ancestral relationship.

The Cryptobranchidae demonstrate significant structural variation within the family. It appears that *Andrias davidianus* is the most advanced, that is, when compared with the Japanese and American species (Figs. 1–3). The throat structures of the genus *Cryptobranchus* indicate a semilarval condition not found in the oriental species. A transition of the hyobranchial apparatus from *Cryptobranchus* through *M. japonicus* to *A. davidianus* is evident in the consolidation of the skeletal elements to form in the latter (*davidianus*) structures that are closely adhering to each other in contrast to the looseness observed in *Cryptobranchus*. The strengthening of these structures may not be just the completing of metamorphosis to full adults; perhaps the increase in the size of adults demanded greater support in the hyobranchial apparatus.

In 1837 Tschudi described the genus *Megalobatrachus* and included in it the giant salamanders of Japan. Because of its size and similar external characteristics, it has been retained by most authors in the genus *Andrias*. After examining the anatomy of various families, and particularly the cryptobranchid *japonicus*, Hilton (1946, 1947) retained the giant salamanders of Japan in the genus *Megalobatrachus*. A comparison of the skeletal structures of the throat shows a consolidation in *davidianus* not seen in *japonicus*. Furthermore, in *davidianus* the first basibranchial is missing and the second has been enlarged to give greater support to associated structures. Based only on the hyobranchial apparatus, the differences are substantial enough to justify the retention of three genera in the family Cryptobranchidae: *Cryptobranchus*—American hellbender, *Megalobatrachus*—giant salamander of Japan, and *Andrias*—giant salamander of China.

Retaining these families (Cryptobranchidae and Hynobiidae) in the same order (Cryptobranchoidea) may be justified based on the primitive characters indicated above of external fertilization and retention of the angular bone in the lower jaw. There are, however, few similarities in the throat anatomy that would indicate a close relationship. Furthermore, the external anatomy does not indicate a close relationship. Both oriental cryptobranchid species are much larger than any of the hynobiids and exhibit an aquatic habitus not as apparent in hynobiids. The fact that hynobiids have diversified as they radiated into various habitats suggests that they have retained a biological vitality not present in the oriental cryptobranchids.

We have been privileged to examine only one specimen of each of the oriental species. There are few oriental cryptobranchid specimens in U.S. collections and these not available for dissection. Therefore, only one side of the throat area was dissected and this to determine only the position of the skeletal parts. A

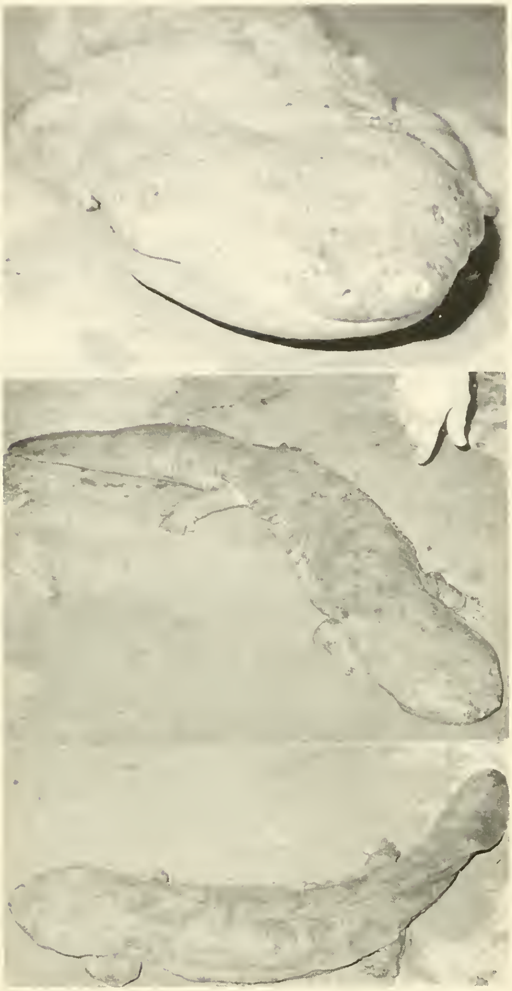

Fig. 8. Photographs of *Andrias davidianus* provided by Dr. James Kezer.

complete examination of the soft tissue and skull may demonstrate additional character variations.

As we examined the three species of the family Cryptobranchidae, we felt a constant impression that we had before us perhaps the most primitive representatives of the salamanders, if not of all Amphibia. The photographs of *A. davidianus* (Fig. 8) indicate little external specialization, with the exception of added skin folds on the body and tail. Aside from the hyobranchial apparatus of the cryptobranchids, which is unspecialized when compared with other families including the hynobiids, those characters listed by Dunn (1926), Morescalchi et al. (1977), and Sessions et al. (1982) provide further evidence that they are an archaic group. Some confirmation of this is also found in the wide distribution in much of the northern hemisphere. Fossil records indicate that the cryptobranchids were extant early in the Cenozoic and appear to have had their origin in late Cretaceous. One might speculate that in those turbulent geological times survival demanded a return to or a retention of a stream habitat, where they have remained to the present with little change. Therefore, one group, *C. alleganiensis*, with its gill bars, has persisted as semilarvae, whereas the asiatic species have evolved to full adults and have increased in size. The fossil record is as yet incomplete and does not provide enough evidence to determine the status of the ancestral stock. The hyobranchial apparatus of *C. alleganiensis* with its retained gill bars does suggest that this species may be similar to the primitive stock. At least it inhabits an area that is geologically old enough to have permitted a long existence in a region affected by relatively little habitat change since late Cretaceous or early Tertiary. If this is true, then the absence of gill bars is a derived character in the Asiatic species.

We find the family Hynobiidae to be a specialized group when compared with the cryptobranchids. We consider the specialized hyobranchial apparatus to be inconsistent with what one would expect from a group having such primitive characters as those indicated above. Using only the data from the hyobranchial apparatus, we find it difficult, in spite of obvious primitive characters, to see a close relationship to the cryptobranchids.

Dunn (1923) states that the

> hyobranchial apparatus of the family (Hynobiidae) agrees with that of the Cryptobranchidae in having the ceratobranchial and epibranchial of the first arch fused into a cartilaginous rod, and in having the ceratobranchial and epibranchial of the second arch present and free.

This generalized statement is far from detailing the specializations in hynobiids as compared with the generalized loose association of the skeletal structures in cryptobranchids. Were we to base conclusions on data obtained from the hyobranchial apparatus of the two families, we would find it more difficult than did Dunn (1923) and others to endorse the idea of a close relationship between them. The slender cartilaginous rod extending from the anterior end of the ceratohyal is unique to hynobiids, as also are the presence of an os thyrodeum and the closeness of the distal ends of the ceratobranchials (Fig. 4); these are not present in the cryptobranchids.

The two families included in the superfamily Cryptobranchoidea (Dunn 1923) both have primitive characters not found in other salamander families, characters that indicate their having descended from a common ancestor. The hyobranchial apparatus does not appear to provide this same relationship. There is good reason to believe that there were several lines of primitive stock in late Cretaceous and/or early Tertiary giving rise to present-day families, with only two retaining some characters that may have been present in several of the ancestral stocks. We find it difficult, based on the hyobranchial data, to see a close relationship. Retaining the Cryptobranchidae and Hynobiidae together in a single superfamily is perhaps more systematic convenience than phylogenetic fact.

Acknowledgments

We gratefully acknowledge the loan of specimens and permission to dissect. Indeed, in view of the scarcity of specimens of these families of salamanders in U.S. museum collections we emphasize our gratitude to the following institutions and the curators who were kind enough to loan us specimens and give permission to dissect the hyobranchial structures: George R. Zug, U.S. National Museum: *Andrias davidianus* USNM 72843, China: "purchased in Shanghai" by Arthur de C. Sowerby, 1925; R. C. Drews, California Academy of Science: *Megalobatrachus japonicus* CAS 16016, Japan: Hondo Island: Mimasaki, J. C. Thompson, 20 September 1905; *Hynobius keyserlingii* CAS 94493–94, USSR: N. Kachatka; *Ranodon sibiricus* CAS 144378-79, USSR: Melkosopochnik (Chinese Turkestan), Ala-tau Mts.; *Hynobius peropus* (larvae) CAS 25741–42, Japan: Hondo Island: Rikuzen Prov.: Shiogama, Victor Kuhne, 1910; *Onychodactylus japonicus* (larvae) CAS 25339, 25348, Japan: Hondo Island: Rikuoku Prov.: Mimaya, Victor Kuhne, 1910; Milwaukee Public Museum: *Hynobius tsuensis* MPM 13907, 13909, Japan: Tsushima: Kechi; *Cryptobranchus alleganiensis alleganiensis* (no data); *Cryptobranchus alleganiensis bishopi* MPM 9294, 4415, Arkansas: Fulton Co., Spring River; Bean Life Science Museum, Brigham Young University: *Cryptobranchus alleganiensis alleganiensis* BYU 40144–45, Missouri: Ozark Co., White River, Max A. Nickerson, November 1971; *Hynobius naevius* BYU 41346, Japan: Kyoto, Doharano, Ukyoky: Hajime Fukada, March 13, 1975. We also acknowledge the kindness of Dr. James Kezer of the University of Oregon who provided photographs of *Andrias davidianus*.

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IMPACT OF CATTLE ON TWO ISOLATED FISH POPULATIONS IN PAHRANAGAT VALLEY, NEVADA

Frances R. Taylor[1], Leah A. Gillman[1], and John W. Pedretti[1]

ABSTRACT.—The presence of cattle at Brownie Spring and Ash Springs in Pahranagat Valley, Nevada, impacted fish populations by causing an increase in ammonia (NH_3) and nitrite (NO_2) levels, an increase in *Pseudomonas aeruginosa* and *Aeromonas hydrophila*, and increased mortality and morbidity. One of the affected fishes, the White River springfish, is listed as endangered by the Department of the Interior. After removal of the cattle from Ash Springs, NH_3 and NO_2 levels decreased and fish populations increased. At Brownie Spring the NH_3 and NO_2 levels are chronically elevated, cattle are still present, and the speckled dace population has not recovered.

As spring systems diminish and human use of land and water increases, endemic fish populations increasingly live precariously between threatened and extinct status. In Pahranagat Valley and elsewhere in the West, a prominent cause of this situation involves the management of water for use by cattle with unrestricted access. Urine and feces from cattle elevate ammonia and nitrites in the water, causing an increase in oxygen needed by nitrifying bacteria and a decrease in oxygen for fish. In addition, ammonia and nitrites are toxic to fish in chronic amounts (Lewis and Morris 1986, Thurston et al. 1986, Sheehan et al. 1986). Direct cattle access to spring systems also results in increases in ubiquitous bacteria such as *Pseudomonas aeruginosa*, *Aeromonas hydrophila*, and coliforms.

This paper examines the effect of cattle on two fish populations in Pahranagat Valley and discusses possible management strategies for spring systems with cattle access problems.

STUDY AREAS

Pahranagat Valley, approximately 18.6 km long and 2 km wide, is about 100 km N of Las Vegas in Lincoln County, Nevada. The valley, bounded by the Pahranagat Mountains on the west and the Hiko Mountains on the east, is drained by the pluvial White River (Hubbs and Miller 1948).

Archaeological data suggest that an aboriginal group presumed to be Shoshonean/proto Numic, probably ancestors of the Numic-speaking Southern Paiutes, entered the valley sometime after 1000 A.D. Caucasians, primarily Latter-day Saints (Mormons), settled the valley in 1865 for the purpose of mining. By 1866, farmers with livestock were moving into the rich farmlands of Pahranagat Valley (Fowler 1973).

Brownie Spring (T5S, R60E, Sec. 26, SE 1/4) is situated at the base of a cliff behind a cattle pasture between Ash Springs and Crystal Springs west of Highway 93 in Pahranagat Valley. The spring headpool measures approximately 8 m by 5 m by 1 m deep with an outflow approximately 50 m long by .5 m wide and less than 10 cm deep. Water temperature fluctuates between 17 C and 21 C, and pH ranges from 7.1 to 7.8. The spring is home to Pahranagat speckled dace, *Rhinichthys osculus* ssp. No exotic fish are found in the spring, although bullfrog tadpoles have been collected occasionally. A native snail, *Physella gyrina* ssp. has been collected. Aquatic vegetation consists of *Nastertium*, *Spirogyra*, and floating algal mats.

Ash Springs (T6S, R61E, Sec. 6), Pahranagat Valley, Nevada, is south of Brownie Spring. It is a warm-water spring with temperatures varying from 33 C at the outflow to 35 C at the headpool. The outflow is on private property, but the headpool is situated on Bureau of Land Management (BLM) land and is developed for recreational camping. One of the two source springs on BLM land is utilized as a "hot tub." There are three endemic fishes in Ash Springs: White River spring fish (*Crenichthys baileyi baileyi*), Pahranagat roundtail chub (*Gila robusta jordani*), and Pahranagat speckled dace (*Rhinichthys osculus velifer*). The White River spring fish and Pahranagat roundtail chub are endangered species pursuant to the Endangered Species Act. The outflow previously supported White River desert suckers (*Catostomus clarki intermedius*) and Pahranagat spine dace (*Lepidomeda altivelis*). Several exotic species, gambusia (*Gambusia affinis*), mollies (*Poecilia mexicana*, *P. latipinna*), and cichlids (*Cichlasoma nigrofasciatum*) have become established in the spring.

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METHODS

Brownie Spring was initially evaluated as a site for a study of population dynamics. It became apparent through the initial eight-month study during 1986 that there were some major problems with the spring system. The system was seined on a monthly basis, and sex ratios, total lengths, and volumes were measured on the fish collected. As the study progressed, the population declined. Because cattle use was obvious, ammonia and nitrite readings were taken and were found to be quite high (Table 1). Live fish brought to our laboratory were in poor health and appeared to be oxygen deprived.

In the summer of 1986, a collection of *C. b. baileyi* from Ash Springs, brought into the laboratory for rearing, was found to be in extremely poor health. Cultures and histopathology showed hyperplasia of the gill lamellae and the presence of *Pseudomonas aeruginosa* and *Aeromonas hydrophila*. Routine evaluation of the spring system revealed cattle at the headpool and elevated ammonia and nitrite levels (Table 1). A culture of the water revealed heavy growth of *Pseudomonas aeruginosa*, *Aeromonas hydrophila*, and an *Enterobacter* sp. Both *Pseudomonas* and *Aeromonas* are considered pathogenic to many species, including humans and fish. *Enterobacter* are common intestinal bacteria. A period of three months was necessary for the fish in the lab to recover and attain reproductive condition.

Population estimates were made of springfish, mollies, gambusia, and cichlids from the summer 1986 through the summer 1988 by seining, marking and recapturing, and snorkeling.

TABLE 1. Ammonia (NH_3) and nitrite (NO_2) levels (ppm) at two springs in Pahranagat Valley, Nevada**. Cattle were removed from Ash Springs between April and June 1987.

	Brownie Spring		Ash Springs	
Date	NH_3	NO_2	NH_3	NO_2
7-86	.28	.7		
8-86	.25	.5	.25	.1
9-86	.28	.8		
2-87	.25	.2	.25	.1
4-87	.25	.2	.25	.1
6-87			.0	<.1
8-88	.25	.25	.0	.0
9-88	.25	.2	.0	.0

**Minimum detectable levels of .2 for ammonia and .1 for nitrite are toxic to fish in chronic amounts.

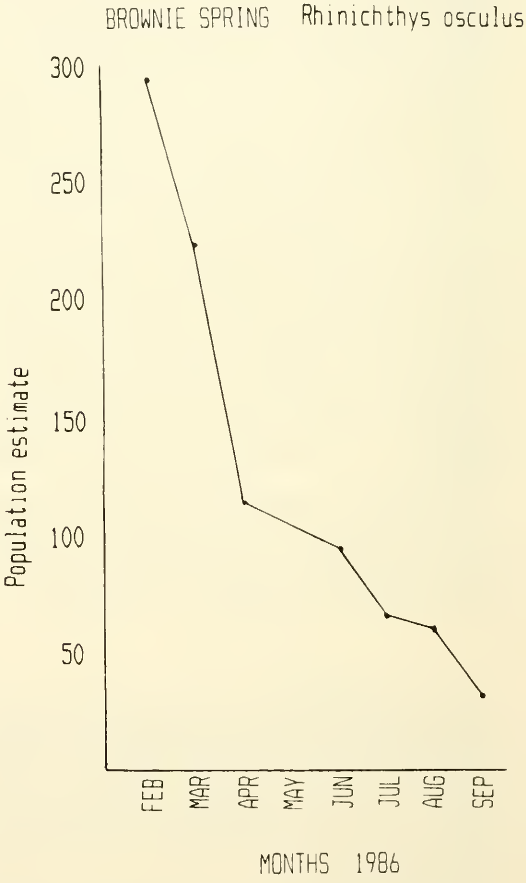

Fig. 1. Population estimates of *Rhinichthys osculus* at Brownie Spring, Pahranagat Valley, Nevada, in 1986.

RESULTS

The effect of cattle on the fish populations of both spring systems appears significant. Within a seven-month period in 1986, the

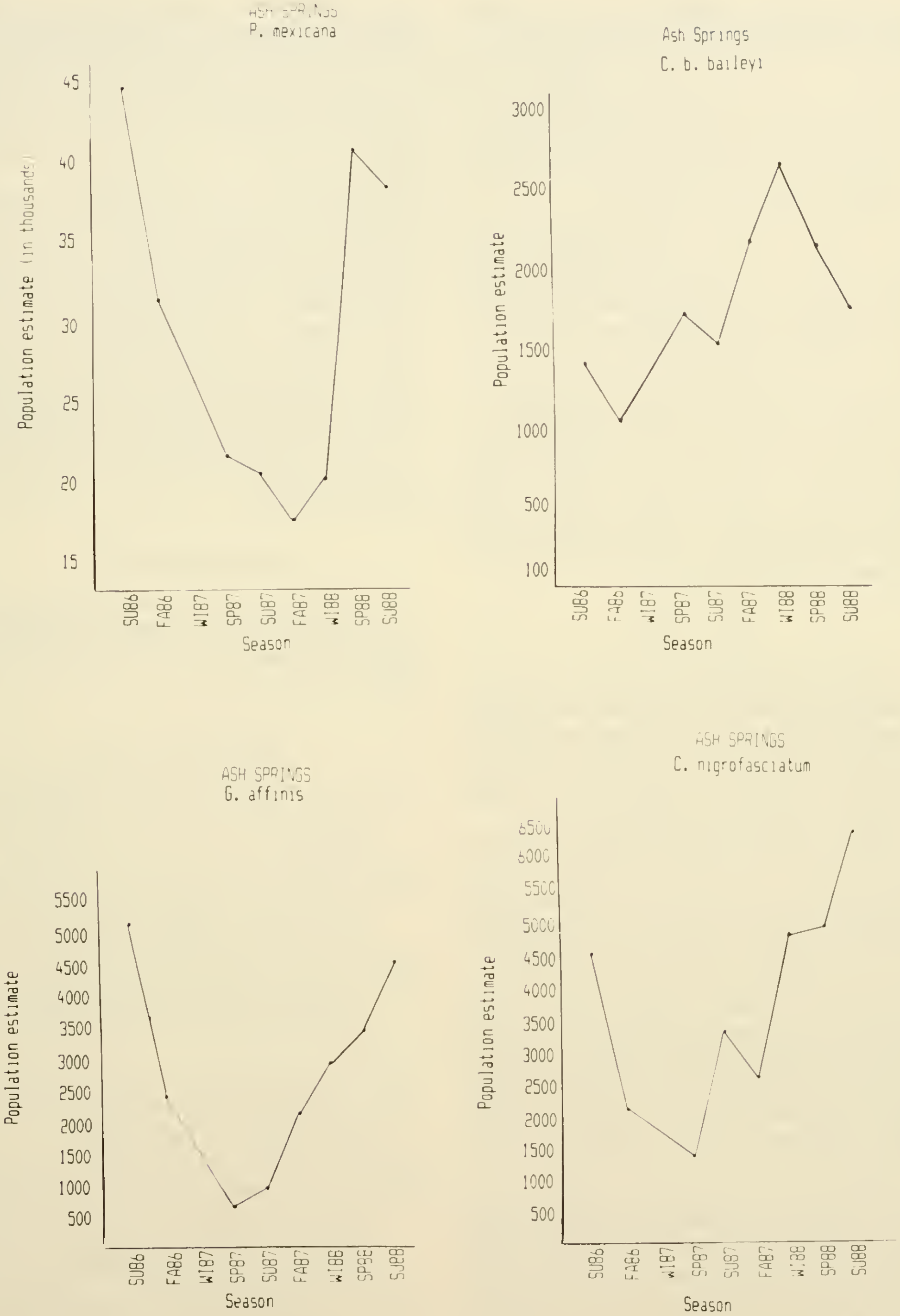

Fig. 2. Population estimates of *Crenichthys baileyi baileyi*, *Gambusia affinis*, *Poecilia mexicana*, and *Cichlasoma nigrofasciatum* at Ash Springs, Pahranagat Valley, Nevada, from summer 1986 through summer 1988.

Brownie Spring population declined from about 284 individuals, including 102 subadults, to 32 individuals with only 14 subadults. The decline was perhaps exacerbated by stress induced by seining (Fig. 1). Since 1986, the population has increased to roughly one hundred individuals. Cattle are still present at Brownie Spring.

Between summer 1986 and spring 1987 when cattle were on the headpool at Ash Springs, there was a marked decline in springfish, gambusia, cichlids and both mollies (Fig. 2). Springfish were least affected, possibly because of their ability to survive conditions of low oxygen concentrations (Hubbs and Hettler 1964). The molly population dropped by over 50%, from approximately 45,000 to about 22,000. Gambusia dropped from 5,000 to 550, and cichlids dropped from 4,500 to 1,300. Cattle were removed in 1987, and by the fall of that year populations of all fishes increased to nearly their 1985 numbers.

DISCUSSION

Cattle at both springs caused an increase in ammonia and nitrites, an increase in bacteria, a possible decrease in oxygen available to the fish, and an increase in fish mortality and morbidity. Removal of cattle at Ash Springs quickly reversed these conditions.

Health of fish collected from springs or streams with unrestricted livestock access should always be suspect. Transporting and holding such fish may require increasing aeration of the water, minimizing stressful factors such as handling and poor water quality (i.e., ammonia and nitrite levels in the water), and instituting antibiotic therapy. We found that fish responded well to Chloramphenicol 250 mg/19 L daily for 7–10 days. It is important to monitor ammonia and nitrite levels daily and change water as needed to maintain low levels.

In a U.S. General Accounting Office report (Duffus 1988), it was found that many riparian areas are overgrazed and in degraded condition because of poor livestock management. These areas provide water, food, shade, and cover for fish and wildlife, which are in some cases threatened or endangered species. Livestock, when unrestricted, tend to congregate in riparian zones for extended periods, eat most of the vegetation, trample the streambanks, and contaminate the aquatic system with urine and feces, all of which increase the mortality and morbidity of aquatic species and degrade water quality. Improved livestock management by fencing or herding can permit seasonal or geographical restrictions.

The Bureau of Land Management has authority and must take the lead in controlling degradation of riparian zones on public lands. They did so at Ash Springs, once the problem was identified. In the frequent instances in which BLM does not require maintenance of an undegraded riparian corridor on public lands, conservation organizations and individuals can speed the process of restoration by invoking the provisions of the Clean Water Act to force BLM to discharge its responsibilities (Braun 1986).

ACKNOWLEDGMENTS

Peter Tuttle provided the population data on Ash Springs. James Deacon critically reviewed the manuscript and provided many helpful suggestions.

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AN EXTANT, INDIGENOUS TORTOISE POPULATION IN BAJA CALIFORNIA SUR, MEXICO, WITH THE DESCRIPTION OF A NEW SPECIES OF *XEROBATES* (TESTUDINES: TESTUDINIDAE)

John R. Ottley[1] and Victor M. Velázques Solis[2]

Abstract.—An extant, indigenous desert tortoise population is reported from the cape region of Baja California Sur, Mexico. This population is described and figured as a new species, *Xerobates lepidocephalus*, distinct from all other North American tortoises including *Xerobates agassizii*, *X. berlandieri*, *Gopherus flavomarginatus*, and *G. polyphemus*. *Xerobates lepidocephalus*, or the scaly-headed tortoise, whose range is known only from an extremely small area in the gulf-drainage mountains just south of La Paz, appears to be a peninsular relict whose closest living relative is probably *X. agassizii*. However, carpal bone affinities connote a close relationship between *X. lepidocephalus* and the Oligocene species *X. laticunea* from Wyoming and Colorado, suggesting that the former species may be one of the more primitive contemporary tortoises of the *Xerobates* lineage. Such evidence indicates that *X. lepidocephalus* is not of vicariant origin resulting from the formation of the cape of Baja California. Scaly-headed tortoises likely ranged, and may yet be discovered, in other medium-elevation mountain ranges of the cape.

The desert tortoise is one of the most recognizable members of the desert biota inhabiting southwestern North America. The most westerly ranging species, *Xerobates agassizii*, has been reported from the deserts of California, Arizona, Nevada, Utah, Sonora, and the extreme northeastern corner of Baja California, Mexico (Van Denburgh 1922, Carr 1952, Stebbins 1966, Auffenberg and Franz 1978a, 1978b). Unfortunately, no confirmed sightings of *X. agassizii* in northeastern Baja California have been made for well over a decade; and, because of the growth of the local human population and the increased use of arable land for farming, the species may no longer exist in this region. Tortoises previously have never been reported from any other portion of Baja California (Norte or Sur).

In early 1987, while seeking information on potential aquatic turtle sites from ranchers residing in the mountain ranges directly south of La Paz, we were told of terrestrial turtle sightings. However, no one with whom we spoke at that time had actually seen a terrestrial turtle nor could they accurately describe where such sightings had been made. We were suspicious of these rumors because, even if substantiated, the occurrence of an indigenous, terrestrial species seemed unlikely, particularly in view of the introduction of slider turtles, *Pseudemys scripta*, into this region by several local families.

In late January 1989 a live tortoise was brought to the La Paz Military Hospital by a rancher who reportedly found the specimen near the Buena Mujer Dam approximately 20 km south of La Paz. In May 1989 we accompanied this rancher to the collecting site and found the fragmented shell of a second tortoise. We made inquiries to residents of that area and were told that although tortoises were only rarely encountered, they were well known in the region. At least two of the families claimed to be direct descendants of homesteaders who arrived in this region during the mid-1800s, all of whom recounted that their ancestors had been familiar with the tortoises, which were wide ranging in earlier time but were now encountered only in the vicinity of a small mountain area known as the Sierra San Vicente. The locals with whom we spoke seemed convinced that the tortoises were indigenous. A comparative evaluation with specimens from other populations convinced us that the Sierra San Vicente population is unique among North American tortoises.

Materials and Methods

During the course of this study, in addition to the type material herein described, we

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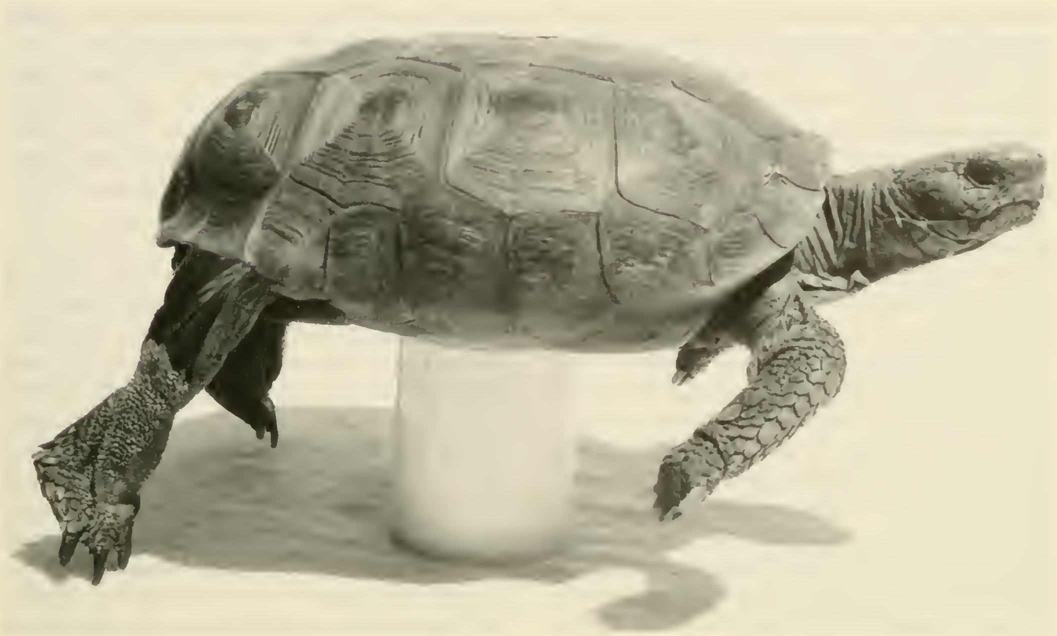

Fig. 1. *Xerobates lepidocephalus:* holotype, BYU 39706, from near the Buena Mujer Dam, Baja California Sur.

examined 29 live specimens of *G. agassizii* (5 specimens from Sonora, 24 from California), 6 live *X. berlandieri*, 1 live *G. flavomarginatus*, and 1 live *G. polyphemus*. Photographs of other specimens were also used to aid in our diagnoses and include: 18 *X. agassizii* (11 from USA and 7 from Sonora), 4 *X. berlandieri*, 3 *G. flavomarginatus*, and 5 *G. polyphemus*. Shell terminology was taken from Woodbury and Hardy (1948) and Carr (1952). Bone terminology follows Auffenberg (1966, 1976) and Bramble (1982). Shell measurements were taken following Woodbury and Hardy (1948), using a high-quality, steel meter stick "in planes parallel to or at right angles to a flat surface upon which the tortoise was resting" (Woodbury and Hardy 1948: 154). Head measurements were taken using a Venier caliper at the widest part of the head (width) and from the tip of the snout to the posterior border of the parietal scales (length). Hindlimb length was taken by measuring the distance from the edge of the plastron to the base of the first nail when the limb was fully extended. Figures depicting cranial, vertebral, and carpal characters were taken from radiographs and/or adapted from Bramble's (1982) ink drawings.

Xerobates lepidocephalus, n. sp.
Scaly-Headed Tortoise

HOLOTYPE.—BYU 39706, an adult female collected by Eusebio Villalobos on 15 January 1989 at the western base of the Sierra San Vicente approximately 1 km N of the Buena Mujer Dam, Baja California Sur, Mexico (Fig. 1).

PARATYPE.—BYU 39707, a reconstructed shell (full plastron and 2/3 of the carapace) of an adult female found approximately 300 m SE of the type locality. Collected by Eusebio Villalobos, Victor Velazques S., and John R. Ottley on 23 May 1989.

ETYMOLOGY.—The species name is taken from two Greek nouns, *lepida* = scaly and *cephala* = head, and refers to the characteristically thickened, raised scales on the parietal and temporal regions of the head.

DIAGNOSIS.—*Xerobates lepidocephalus* is distinguished from all other North American tortoise species (*Xerobates agassizii, X. berlandieri, Gopherus flavomarginatus*, and *G. polyphemus*), as well as virtually all testudinids, in lacking enlarged scales on the frontal and prefrontal regions (intersupraoculars); these scales in *X. lepidocephalus* are smooth, small, and subequally sized (with at least four frontal scales separating the orbits; rarely more than two frontals occur in other *Xerobates* and usually only one in *Gopherus*). *Xerobates lepidocephalus* is further distinguished in having thickened, raised, nonsloughing scales covering the parietal and temporal regions of the head. The holotype of *X. lepidocephalus* also possesses well-fused 4th and 5th carpal bones (a characteristic previously observed only in Oligocene *X. laticunea*) and lacks a distinct pisiform (also absent in *G. flavomarginatus* and *G. polyphemus*).

DESCRIPTION OF TYPE.—An adult female with the following measurements: carapace length 229 mm, carapace height 89 mm, carapace width 181 mm, head length 51 mm, head width 37 mm, hind limb length 84 mm. Ratios: carapace height to length .388, carapace width to length .790, head length to carapace length .222, hind limb length to carapace length .367. Coloration (in life) as follows: carapace dusky yellow-brown with slightly darker areolae, anterior halves of lateral marginals slightly lighter; plastron dirty yellowish tan; nonscaly skin around limbs light cream-yellow (most vivid around hind limbs), skin around neck region light yellowish brown, skin with scales darker and scales same color as carapace; heavy scales on limbs and around tail same color as carapace; scales on top of head (parietals, temporals, frontals, and prefrontals) dirty yellowish tan, mottled with slightly darker brown; other portions of head approximate color of carapace. Plastral scutes lack alveoli (excessively worn), carapace scutes with distinct alveoli, but vertebrals and lateral marginals have smooth spots (worn). Head scales on frontal and prefrontal regions small, nearly equal in size, with a minimum of 4 intersupraoculars. Parietal and temporal scales thickened and distinctly raised to as much as 2 mm, abruptly differentiated from other dorsal head scales. Anterior forelimb scales flattened, subequal in size, with a rapid transition to small scales just above the wrist; nails rounded and peglike. Bones of antebrachium as follows (taken from X ray): phalangeal formula 2-2-2-2-1, medial and lateral centrale fused, 1st and 2nd carpals fused, 4th and 5th carpals fused, pisiform appears to be fused with ulnare; radius in contact with 1st and 2nd carpals.

RANGE.—Known only from the Sierra San Vicente region, approximately 1.5 km north of the Buena Mujer Dam, 20 km (by air) south of La Paz, Baja California Sur, Mexico.

VARIATION OF CHARACTERS.—Although only one complete specimen of *X. lepidocephalus* is currently available for meristic scale analysis, its head scale characteristics are unique to the extent that there is an extremely low degree of overlap with other species. For example, all North American tortoises (as do virtually all tortoises) have enlarged frontal or prefrontal plates and relatively flattened scales covering the parietal and temporal regions. *Gopherus* spp. generally have two large frontal plates (one in front of the other) that cover most of the frontal (intersupraocular) and prefrontal region, either one of which may be divided. *Xerobates agassizii* and *X. berlandieri* usually possess at least one pair of enlarged frontal plates that may vary in size and shape, and generally cover or partially cover only the frontal region; smaller intersupraoculars (occasionally granular scales) may also be juxtaposed with these plates, with as many as 4 to 6 scales between the supraoculars. One specimen of *X. berlandieri* (collection of S. Veverka) had divided frontal scales to the extent that only one slightly enlarged scale remained. Scales covering the parietal and temporal regions tend to be slightly larger and smoother in *Gopherus* spp. than in *X. agassizii* and *X. berlandieri*, and generally show more signs of sloughing in these latter species; in all of these tortoises the only notable difference in the nature of the scales from the frontal to the parietal regions is a size change. In *X. lepidocephalus* there is a very marked and abrupt change from the flattened frontal scales to the vividly thickened and raised parietals; these latter scales give the appearance of flat-topped cobblestone. Raised and/or thickened parietal and temporal scales are unknown in *Gopherus* spp. and *X. agassizii;* however, one specimen of *X. berlandieri* (collection of L. Greene) had a few slightly raised scales bordering on the parietal/temporal transition.

The fusion of the 4th and 5th carpal bones and the lack of a distinct pisiform observed in the holotype of *X. lepidocephalus* are of uncertain diagnostic value. Both this type of carpal fusion and unfused 4th and 5th carpals are known in Oligocene *X. laticunea* (Bramble 1982). The apparent fusion of the pisiform with the ulnare in the *X. lepidocephalus* holotype may be the result of ontogeny and may vary a great deal within this and other species (Charles Crumly, personal communication, 1989). Whether or not manus bone morphology is of true diagnostic value in *X. lepidocephalus* will depend on the revelations of further study.

DISCUSSION

During the 19th century three species of North American tortoises were described in two genera: *Gopherus polyphemus* Daudin (1801, Auffenberg and Franz 1978e), *Xerobates berlandieri* Agassiz (1857, Auffenberg and Franz 1978c), and *X. agassizii* Cooper (1863, Auffenberg and Franz 1978b). According to Van Denburgh (1922), Stejneger (1893) was the first to consider all three of these forms as congeners, an assessment that persisted for nearly 90 years. Legler (1959) described *G. flavomarginatus* (Auffenberg and Franz 1978d), a species he recognized as being closely related to *G. polyphemus*, but discussed relationships with other North American species in the congeneric sense as well.

More recent compendia on desert tortoise taxonomy have revived arguments for and against recognition of separate genera. Auffenberg (1966, 1976) observed that North American tortoises naturally fell into two species groups. Bramble (1982) took this one step further and placed those groups into separate genera in the following associations: *polyphemus* and *flavomarginatus* under *Gopherus*, and *agassizii* and *berlandieri* under a newly erected genus, *Scaptochelys*. Bramble based this level of recognition on what he interpreted to be eight bilaterally unique, diagnostic characters. The results produced two distinct, functional species groups: specialized burrowers, *Gopherus;* and, more generalized diggers, *Scaptochelys*.

Bour and Dubois (1984) concurred with Bramble's diagnoses for two genera but demonstrated that the position of *Scaptochelys* was already occupied by Agassiz's (1857) genus *Xerobates* (Cooper 1863, True 1882). Crumly (1984, 1985, 1988, personal communication, 1989) noted the uniquely specialized characters shared between *G. flavomarginatus* and *G. polyphemus* but found that *X. agassizii* and *X. berlandieri* did not appear to share a similarly close relationship with one another since they both manifest many of the primitive or "transitional" characters that have become specialized in *Gopherus* (i.e., the presence of a sacular otolith). For these reasons Crumly opted for a single genus, *Gopherus*, to encompass North American tortoises.

The dispute over generic status stems from differing interpretations over the importance of the shared primitive characters. In a strictly morphological sense the shared primitive characters strongly suggest monophyly and therefore the recognition of a single genus. However, when compared with the more derived and shared functional characteristics of each species group, a two-genera interpretation can be argued (Bramble 1982, Lawler 1986, Van Devender 1986, personal communication, 1989). Further, the fossil record indicates that two lineages were distinguishable by the Middle Miocene and have remained largely allopatric since that time (Bramble 1982, Van Devender 1986, Lamb et al. 1989). Lamb et al. (1989) also observed that the qualitative pattern of mitochondrial DNA phylogeny estimates for North American tortoises were substantial, thus adding strength to the recognition of separate genera. At present there is enough evidence to defend either taxonomic point of view; thus the matter of separate genera becomes more a question of how one defines the data. In our opinion, evidence for the recognition of two genera more fully conveys the unique, adaptive histories of each tortoise group: sandy soil burrowers or gopher tortoises, *Gopherus*, and compact soil diggers or desert tortoises, *Xerobates*.

Although head scales (Fig. 2) clearly distinguish *X. lepidocephalus*, comparative similarities of the carpal morphologies (Fig. 3), cranium, and vertebrae (Fig. 4) ally this species with the *Xerobates* group; similarities in shell meristics suggest that its closest living relative is *X. agassizii*. However, the uncommon fusion of the 4th and 5th carpals, a character that *X. lepidocephalus* shares with Oligocene *X. laticunea*, may suggest a close (if not closer) ancestral relationship. Because primitive head scale morphologies are not well known and because *Gopherus* manifests the more primitive manus bone characteristics of North American tortoises, it is unclear whether the head scales and manus bones of

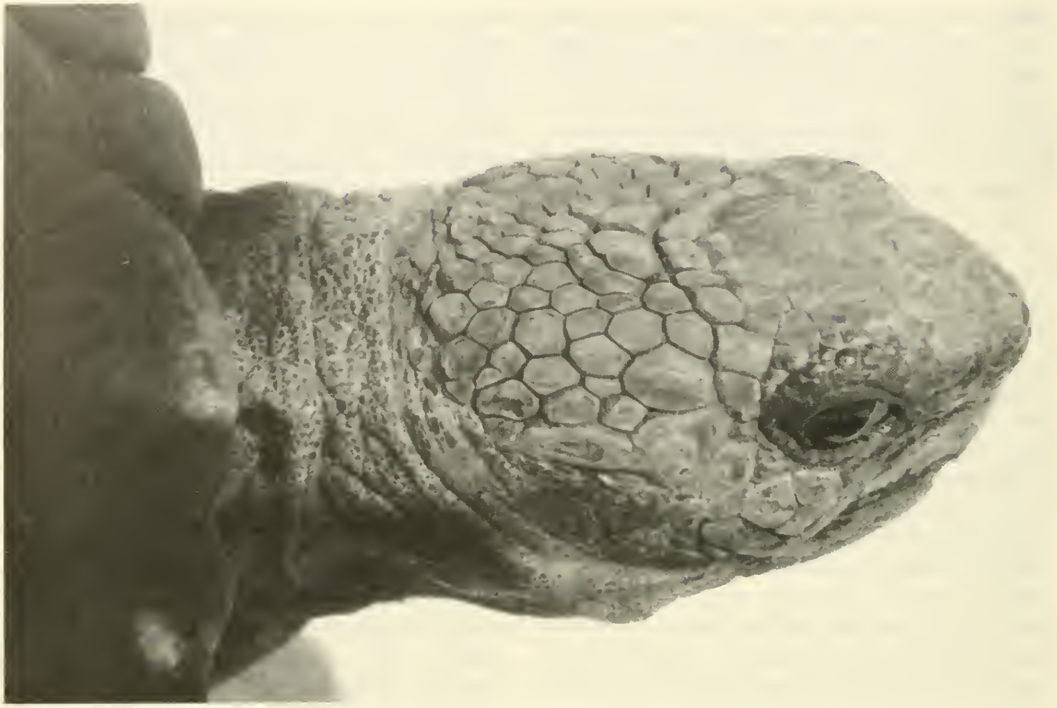

Fig. 2. Dorsolateral view of the head of BYU 39707, showing the small, smooth frontal and prefrontal scales and the abrupt transition to the thickened, raised parietal and temporal scales.

X. lepidocephalus reflect primitive or derived conditions within the genus.

Owing partly to the unresolved taxonomic status of *X. agassizii* populations from Sonora and Sinaloa, the biogeographic origin of *X. lepidocephalus* remains somewhat unclear. Although the known range of *X. lepidocephalus* is limited to the northeastern cape region, the following cursory evidence suggests that it is probably not a cape vicariant: (1) *X. lepidocephalus* may be closely related to *X. laticunea* from Oligocene deposits of Wyoming and Colorado, (2) a population at the southern range terminus of mainland Mexican *X. agassizii* appears to represent a distinct taxon (Lamb et al. 1989) less closely related to *X. lepidocephalus* than this latter species is to northern populations of *X. agassizii*, (3) no fossil tortoises have been found in the Baja California cape or in the region of Jalisco, Mexico, the origin of the cape land mass, and (4) head scale meristics of *X. lepidocephalus* overlap slightly with those of the eastern species *X. berlandieri*. However, because extant *Xerobates* spp. penetrate well into the tropical thorn forest of Sonora and Sinaloa, the possibility of a once more southerly ranging ancestor should not as yet be totally discounted. Despite such arguments, the bulk of current evidence suggests that *X. lepidocephalus* entered Baja California from a more northerly origin, perhaps vicariantly via fragmentation of mid-peninsular land masses and/or at the base. This species is now an isolated relict that may comprise several disjunct peninsular populations.

Although it is surprising that a relatively visible species such as a tortoise passed undetected by naturalists for so long, the discovery of the Baja tortoise is not unlike that of *G. flavomarginatus*. *Xerobates lepidocephalus*, though not currently used as a meat source as is *G. flavomarginatus* (Legler 1959), is well known to the natives; both species occur in areas of considerable human activity. The countryside around the Buena Mujer Dam is dotted with ranches, and the dam itself is visited frequently by residents of La Paz and the San Juan plain. Also, the ranges of both species appear to be restricted to higher

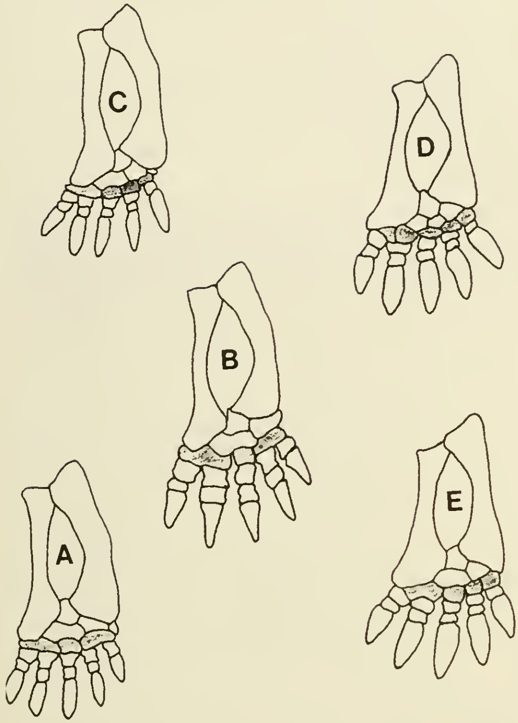

Fig. 3. Comparative morphology of the fused and separate right manus carpal bones (shaded), which number sequentially from left to right, of *Xerobates* and *Gopherus:* A and C, Oligocene *Xerobates laticunea;* B, holotype of *X. lepidocephalus;* C, *X. agassizii* and/or *X. berlandieri;* D, *Gopherus polyphemus;* and E, *G. flavomarginatus.* Figures not to scale.

elevations. Nevertheless, skepticism abounded as to the origin and status of both species. For example, Grant (1960) severely challenged the origin of the type specimens of *G. flavomarginatus* and the taxonomic status of this species. Similarly, local naturalists from La Paz, as did we, initially found it difficult to accept the idea that a geographically restricted tortoise population in the cape region of Baja California was anything other than introduced. Though little is known about the origin and current distribution of *X. lepidocephalus*, its indigenous status is strongly buoyed by its dramatic diagnostic morphology; and, despite the fact that the meristics were taken from a single specimen, the chance that two, and possibly three, heretofore unknown diagnostic characters could be anomalies is probably very low.

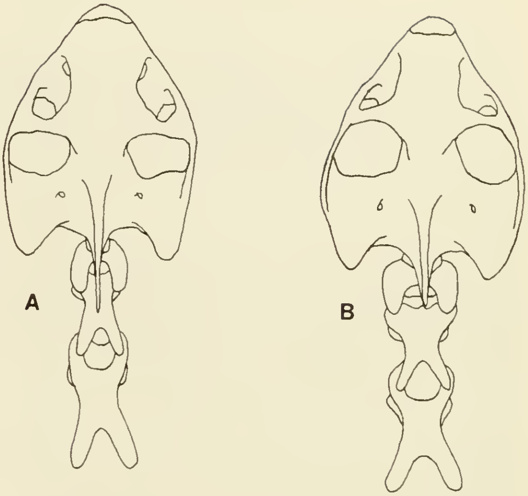

Fig. 4. Dorsal view of the cranium and vertebrae of *Xerobates lepidocephalus:* A, taken from life-size radiograph of the holotype, BYU 39706; B, the cranium and vertebrae of *Xerobates agassizii*, adapted from Bramble (1982). Figures approximate life size.

Seasonal activity of *X. lepidocephalus* is believed to correspond primarily with the summer and fall rains, an observation corroborated by several local ranchers. The locals also noted that tortoises were infrequently encountered even at that time of the year and that they were usually seen on sloped or hillside areas; no one could recall having seen burrows. Thomas Van Devender (personal communication, 1989) stated that tortoise populations around Tucson, Arizona, are termed "summer rainfall tortoises" because of their seasonal activity; these tortoises are rarely found away from hillsides and do not burrow to avoid water runoff and flooding, particularly during the monsoon season. The late summer activity, suggested habitat preference, and lack of burrows reported by the Sierra San Vicente natives indicate that *X. lepidocephalus* is probably a "summer rainfall tortoise" as well.

At present the range of *X. lepidocephalus* is known only from the rocky foothills of the Sierra San Vicente. This area comprises less than two square kilometers. Eusebio Villalobos told us that during his 15 years in the area he had seen only five or six tortoises. If the observations of the native ranchers are correct, the Sierra San Vicente may house the last vestige of this species in the cape region.

ACKNOWLEDGMENTS

We thank Eusebio Villalobos, Jésus Velázques S., Leticia Velázques, and Scott Selstad for their help and companionship in the field. For the loan of specimens and help in obtaining photographs of specimens we thank James Buskirk, Kevin Yates, James and Sandra Veverka, Cuca Espinosa (of San Ignacio, Baja California Sur), and Lillian and Max Greene. Drs. Ron Adair and Steve McHale graciously extended the use of their X-ray lab to us; and, aided by their lab personnel, Laura McDonald and Tammy Whitten, we obtained the radiographs from which the skeletal figures were taken. Dr. Charles R. Crumly graciously shared his provocative and well-founded taxonomic perspectives. We extend our appreciation to Dr. Thomas Van Devender, whose wealth of field observations and insights on desert tortoises he shared with us helped to confirm our meager field data on the Baja California species. The lucid commentaries of James Buskirk, Sandra Veverka, Dr. Charles H. Lowe, Jr., and Howard Lawler also added greatly to this study. Reviews by Dr. Wilmer W. Tanner and Dr. Stephen L. Wood aided the clarity of the manuscript. We are greatly indebted to Jorge Rodríguez R., José Luis Genel G., and Victor Haus V. of the Subdelegación de Ecología Departamento de Aprov. Inspecc. y Vig. Ecologica (SEDUE) of Mexico City, La Paz, and San José del Cabo, in conjunction with Romel Cota and Arturo Gomez C. of the III Ayuntamento de los Cabos, Delegación Municipal of Santiago, as well as the commandant of the La Paz Military Hospital for helping us obtain collecting and export permits (numbers 03.02.257/88 and 01.315/89) for our specimens. We also thank U.S. Customs Service for their cooperation.

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STATUS OF *SPEA STAGNALIS* COPE (1875), *SPEA INTERMONTANUS* COPE (1889), AND A SYSTEMATIC REVIEW OF *SPEA HAMMONDII* BAIRD (1839) (AMPHIBIA: ANURA)

Wilmer W. Tanner[1]

Abstract.—In this report emphasis is placed on the dorsal skull characters of the genus *Spea* and the three species, *bombifrons*, *hammondii*, and *intermontana*. *Spea hammondii* is a polytypic species with at least three subspecies, *hammondii*, *multiplicatus*, and *stagnalis*, each of which is described and the distribution indicated. Drawings and photographs of skulls are provided for each species, with *hammondii* and *intermontana* receiving special consideration.

Few North American amphibians have had such a varied and uncertain systematic past as that of the spadefoot toad. Recent fossils have aided researchers in understanding the relationships between historic and modern species. These relationships strongly suggest that all spadefoot toads be retained in the family Pelobatidae. Cope (1875), based on material available to him, placed American species in the family Scaphiopodidae including two genera, *Scaphiopus* Holbrook (1836) and *Spea* Cope (1875).

The purpose of this study is a review of the species and/or subspecies of those taxa referable to the genus *Spea;* included are *S. bombifrons* Cope, *S. intermontana* Cope, and *S. hammondii* Baird. It is not the intent of this study to become involved in further justification of the family or a review of the generic taxa. This has been repeatedly discussed by numerous authors (Cope 1875, 1889, Tanner 1939, Zwiefel 1956, Tihen 1960, Holman 1963, Kluge 1966, Estes 1970, Brown 1976, Tanner 1989, and others).

The fossil record for the genus *Spea*, as reported by Holman (1963), Tihen (1960), Kluge (1966), Estes (1970), and others, indicates that *Spea* has been an identifiable group in the Great Plains of central North America since the Lower Miocene (*S. neuter*, Kluge 1966) and the Early Oligocene (*Eopelobates grandis*, Zweifel 1956). If we accept the conclusions reached by Kluge (1966) that the dichotomy between *Scaphiopus* and *Spea* may have occurred as early as Late Miocene and has apparently continued to differentiate to the present, and since we can recognize each genus morphologically and can also delineate distinct differences in the life history of each, then it seems logical to recognize each generic group as distinct rather than to retain them in an inconsistent taxonomic relationship.

I consider the skull of *Scaphiopus*, with its dermal plates, to be primitive. This character is, I believe, more than a slight difference when compared with the skull of *Spea*. The loss of the dermal plates in *Spea* is considered a derived character. Obviously there are similarities that relate *Scaphiopus* and *Spea*, similarities that place them both in the North American branch of the family Pelobatidae. Based on the distinct differences in the skulls and other morphological, life history, and ecological differences discussed by Bragg (1944), Blair (1955, 1956), Zweifel (1956), and Kluge (1966), I am persuaded to accept *Spea* as a genus rather than to continue dealing with a *Scaphiopus*-*Spea* complex (Tanner 1989).

The skull and external characteristics are well documented for *bombifrons* and *intermontana*. There is doubt as to whether *hammondii* has been adequately examined, particularly with regard to the skull characters and their relationships to the populations occurring in areas in southwestern United States and western and southern Mexico. Tanner (1989) demonstrated that the skull characters of *Spea hammondii* occur in a large series of populations, including those from southwestern United States and northwestern Mexico. By including those populations having a large frontoparietal fontanelle in one species

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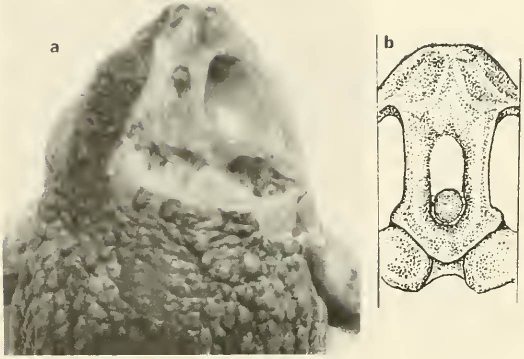

Fig. 1. *Spea hammondii stagnalis* Cope (or an undescribed subsp.): a, 3 mi (hwy rd) N Fronteras, Sonora, Mexico, UAZ 39069 (photo of dorsal view of skull); b, interorbitals and fontanelle complex enlarged to show separate thin bone in posterior part of fontanelle.

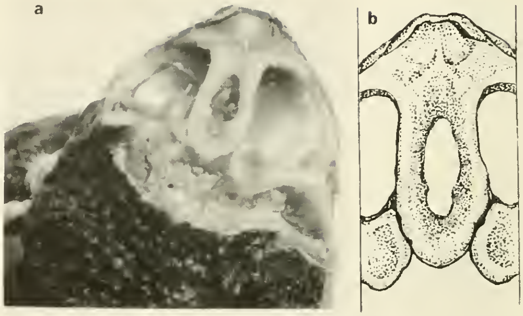

Fig. 2. *Spea hammondii hammondii* Baird: a, San Diego, San Diego Co., BYU 2141 (dorsal view of skull); b, enlargement of interorbitals, adjoining bones, and their position to each other and the orbit. Note that the interorbitals are flat, without bosses of bony protuberances extending into the fontanelle.

(*hammondii*) and recognizing the external and ecological variables as subspecific characters, some systematic order can be realized.

Spea hammondii does not have the skull modification seen in *bombifrons* or *intermontana*. In all specimens examined the interorbitals are narrow without enlargements, and with a large interorbital fontanelle between them. Thus, in adults the area between the orbits is flat, or nearly so, and is covered by skin and layers of glandular and connective tissue that serve as a covering over the fontanelle and the cerebral hemispheres that lie below and are visible when the fontanelle is exposed. Two variations were noted. In a specimen from Sonora (UAZ 39069, Fig. 1), a small, circular, flattened bone is fitted into the enlarged posterior part of the fontanelle. It is attached to the interorbitals by fine strands of connective tissue. In specimens from California and Baja California the fontanelle is so positioned as to extend to or beyond the posterior edge of the orbits, a condition not often observed in other populations of *hammondii* nor in *bombifrons* or *intermontana* (Fig. 2).

In spite of these modifications, *hammondii* has retained a simplified skull that implies a primitive condition with few derived characters. If *hammondii* represents the primitive species in the genus *Spea*, it becomes more difficult to assign a population or subspecies as the rootstock of the species and of the genus.

Skull characters (i.e., the relationships of the frontoparietal fontanelle, its size and position) do not vary greatly within the wide range sampled (western Texas west to southern California and south in the adjoining Mexican states of Chihuahua, Sonora, and Baja California). Single skulls from populations in Nuevo León, Morelos, and Oaxaca also appear to be part of the *hammondii* assemblage. On the bases of variations in the frontoparietal area of the skull, three species of the genus *Spea* are recognized: *hammondii*, for its narrow, unmodified interorbitals that are separated by a large interorbital fontanelle (Fig. 3); *bombifrons*, for its enlarged boss on the anterior of each interorbital, a reduced interorbital fontanelle posterior to the enlarged bosses, and a groovelike channel between the bosses extending as a depression between the nasals (Fig. 4); *intermontana*, for a general enlargement of the interorbitals without a boss, with the interorbitals arched medially, and with thin bone extending mesially to reduce or eliminate the fontanelle (Fig. 5). In both *bombifrons* and *intermontana* the interorbital fontanelle is reduced in size anteriorly, leaving a smaller fontanelle.

There is also an additional feature that is characteristic of the species of the genus *Spea*, in that the spade is wedge-shaped. This is in contrast to members of the genus *Scaphiopus* in which the spade is sickle-shaped. The basic ground color for the genus *Spea* is a dark gray with a tinge of dark greenish yellow (for color patterns and comparisons see Stebbins 1985, plate 10). In some specimens there may be light stripes or spots on the dorsum, but the pattern is not a reticulation as is observed in most specimens of *Scaphiopus couchii*. There

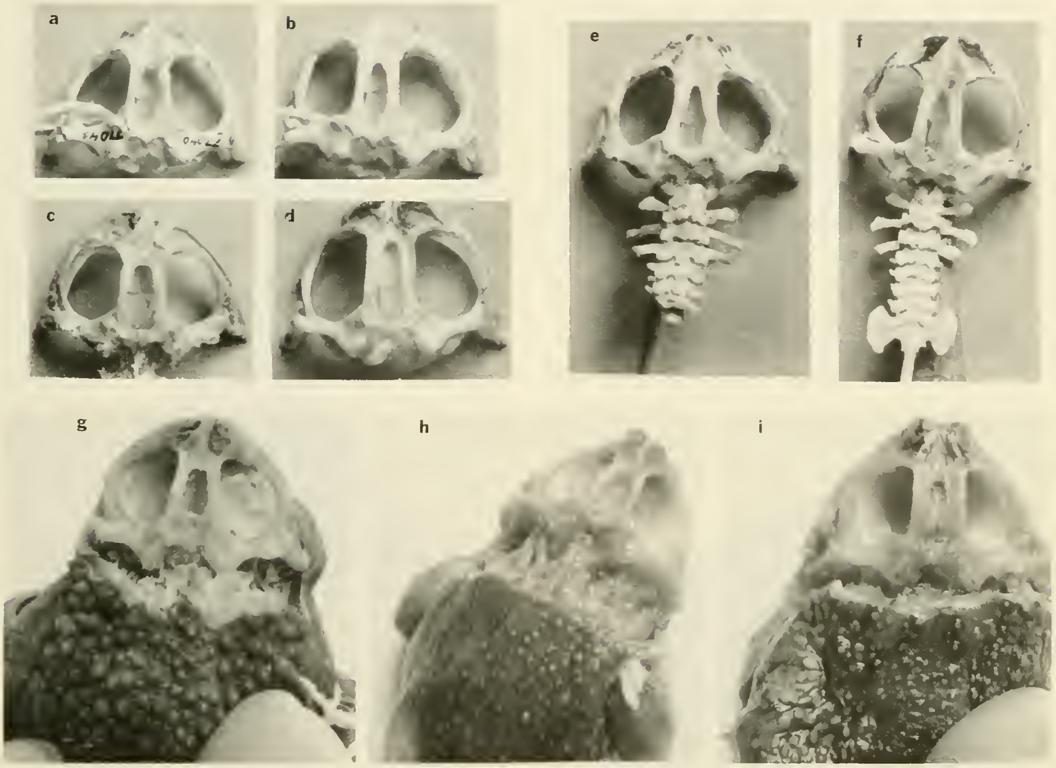

Fig. 3. A series of representative photos of the dorsal aspect of the skulls of *Spea hammondii:* a, *S. h. hammondii*, San Joaquin Range Expt. Station, Madera Co., California, MVZ 77040; b, *S. h. hammondii*, Corral Hollow Rd, 5 mi W to 5 mi E Alameda–San Joaquin Co. line, California, MVZ 145191; c, *S. h. stagnalis*, Brewster Co., Texas, KU 10276; d, *S. h. multiplicata*, 3.5 km W Cuaulixco, Morelos, Mexico, KU 84890; e, *S. h. multiplicata*, 33.6 km S San Roberto, Nuevo León, Mexico, KU 117350; f, *S. h. multiplicata*, 6 km SE Oaxaca, Oaxaca, Mexico, KU 117345; g, *S. h. multiplicata*, Chuhuichupa, Chihuahua, Mexico, BYU 15406; h, *S. h. stagnalis*, 18.8 mi N Cd. Durango, Durango, Mexico, BYU 15526; i, *S. h. stagnalis*, Montezuma Creek, San Juan Co., Utah, BYU 18460.

is an indication that *S. couchii*, whose distribution overlaps the distribution of *bombifrons* and *hammondii*, is larger in the adult S-V length. This has been my observation from specimens of both genera collected in Chihuahua, Mexico. Certainly, in our field surveys, we have had no difficulty differentiating *Spea* specimens from *Scaphiopus couchii*, based solely on size and color pattern.

It may not be possible to differentiate all specimens of *Spea* to their proper taxon by external examination. This is particularly the case in some subspecies of *hammondii*. Perhaps, for this reason, Cope (1875) used skull characters in separating the species in the genus *Spea*. The species *S. bombifrons* will be dealt with briefly as it is taxonomically well established and its distribution indicated by Conant (1975) and Stebbins (1985). Most of this study will deal with the species *hammondii* and *intermontana*. Within these species an attempt is undertaken to compare skull characters, particularly from the dorsal aspect, to visualize variation in the populations that occur in numerous valleys throughout much of western United States and Mexico.

The species *Spea bombifrons*, with an enlarged boss at the anterior of the interorbitals, is uniquely different from all others in the genus (Fig. 4). Our collecting records indicate that it prefers a grassland habitat in contrast to *hammondii* and *intermontana*, both having been found in a variety of habitats. Although its geographical range is primarily in the grasslands of the Great Plains, it is now found in suitable habitats in eastern Arizona, most of New Mexico, and in the San Juan River basin of southern Colorado and southeastern Utah.

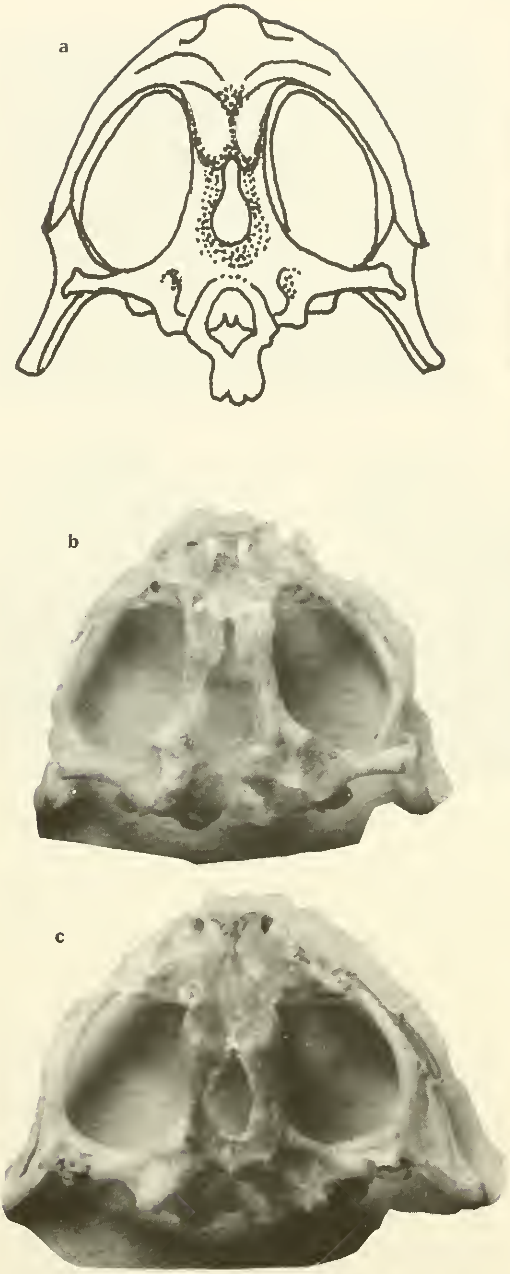

Fig. 4. *Spea bombifrons*, dorsal view of the skulls: a, Navajoland, Apache Co., Arizona, LACM 127299; b, Las Cruces, Dona Ana Co., New Mexico, KU 73382; c, Rexroad Ranch, Meade Co., Kansas, KU 22145.

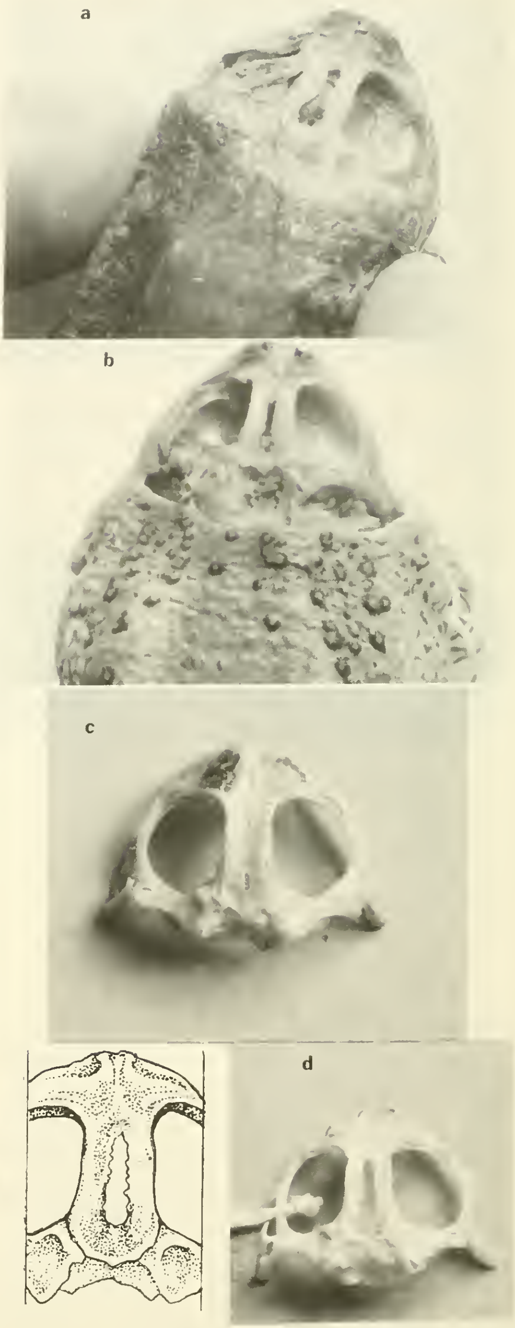

Fig. 5. *Spea intermontana:* a, dorsal view in which the fontanelle is nearly closed, Hog Springs 15 mi NW Hite Ferry, Garfield Co., Utah, BYU 16647; b, Helper, Carbon Co., Utah, BYU 2060; c, Cherry Creek, Juab Co., Utah, BYU 9071; d, on Hwy 168, 0–10 mi E of jct with Hwy 395, Mono Co., California, MVZ 145204. The insert depicts the intrusion of bony projections along the inner edges of the interorbitals.

Specimens examined throughout this wide area show a very similar series of skull characters. This is in contrast to my findings in *hammondii*.

The wide-ranging *Spea hammondii* has modifications not only in the skull characters (Fig. 3) but also in its external anatomy and life history. A brief discussion of the above characters will aid in understanding the systematics of *S. hammondii*.

Skulls examined from specimens representing populations of *hammondii* in Mexico (Nuevo León to Baja California and south to Oaxaca) and southwestern United States (Texas west to California) all have a large interorbital fontanelle, with the interorbitals narrow, relatively flattened dorsally, and without modifications (Fig. 3). Size and position in relation to the orbits vary. In the California and Baja California populations the fontanelle may extend beyond the posterior margins of the orbits. In other populations (Arizona and New Mexico, for example) the fontanelle is shorter, usually not extending beyond the posterior margins of the orbits. Although the size of the fontanelle varies with the size of specimens, its position in relation to the orbits usually does not.

The development of a flattened disc of bone in the posterior of the fontanelle in one specimen from a population in Sonora (UAZ 39069) may indicate a strengthening of the dorsal skull area as has occurred in both *bombifrons* and *intermontana*. This may also be a further indication that *hammondii* is the primitive group in the genus *Spea*.

The species *Spea hammondii* has extensive population segments, many of them isolated geographically as well as ecologically. Under these conditions it is not surprising that subspecies can be recognized. It has not been possible to examine the numerous Mexican populations in the eastern states (Nuevo León) and populations south of Durango, and to this extent this report is incomplete. This report is a preliminary study involving limited data from widely dispersed populations. A far more detailed study, including added field data and considerably more morphological and ecological data, would be necessary to fully understand the genus *Spea*. A comparison of the external anatomy of specimens from the mountains of western Chihuahua with those in south central Mexico suggests that additional subspecies may exist in Mexico. However, materials available have provided data that suggest the following subspecies of the species *S. hammondii* be recognized.

Spea hammondii hammondii Baird
Hammond's spadefoot

Diagnosis.—Interorbitals narrow, widely separated by an enlarged fontanelle; fontanelle usually extending beyond the posterior margin of orbits (Fig. 2); dorsal tubercles small, not numerous on back; large, S-V 55–65 mm; adapted to a late-winter or early-spring (March) breeding season to correspond with the rainy season.

Distribution.—In the central valleys of California and south into northern Baja California. This subspecies does not extend into the deserts of southeastern California and is separated from the subspecies in Arizona by extensive deserts.

Spea hammondii stagnalis Cope
Desert spadefoot

Diagnosis.—Interorbitals narrow, fontanelle to but usually not beyond the posterior margin of the orbits (Fig. 3); dorsal tubercles usually small and widely separated; smaller, S-V 50–55 mm; color with light spots or irregular dorsolateral stripes; adapted to breeding when late-spring or summer rains occur, varying with the occurrence of rainstorms in various areas from May to September.

Distribution.—In central and southern Arizona south of the Mogollon Rim; south into central Sonora; east into New Mexico, and north to include the San Juan River basin of New Mexico, southwestern Colorado, extreme southeastern Utah, and a corner of northeastern Arizona; east into western Texas and presently including isolated populations in Nuevo León, Mexico; south from New Mexico into Chihuahua and Durango, Mexico. In the Mexican states of Chihuahua and Durango populations occur in valleys along the eastern edge of the Sierra Madre, with a distribution in a relatively narrow belt between the mountains to the west and the eastern deserts.

Spea hammondii multiplicata Cope
Mexican mountain spadefoot

Diagnosis.—Interorbitals narrow, fontanelle large, usually not reaching posterior margins of orbits (Figs. 3d–g) (the skull structures for most populations south of Durango were not examined); dorsal tubercles greatly enlarged and numerous on dorsum of body;

color usually a uniform dark greenish brown; smaller, S-V 50–55 mm; adapted to breeding during the late-spring and summer rains (this varies from south to north and with elevation).

Distribution.—Occurs in the high mountains and plateaus of western Chihuahua and Durango. Populations south of these states appear to be a part of this subspecies. The range may, as noted by Smith and Taylor (1948), extend into central and southern Mexico.

Spea intermontana Cope
Great Basin spadefoot

Diagnosis.—Interorbitals enlarged, arched medially, and convex between orbits, interorbital fontanelle greatly reduced by mesial extensions of the interorbitals. In some individuals only a small remnant of the fontanelle remains, and it is always the posterior part. No enlarged boss is present. There is a convex enlargement of the interorbitals near the orbits that produces rainbowlike arches between the orbits (Fig. 5). Between the interorbitals is a concavity with variable-sized fontanelles (this depends on the individual and population) that is filled with glandular and connective tissue. In adults this may appear as a boss between the orbits, but it is an entirely different structure from that of *bombifrons*. Larger, S-V 55–60 mm; color pattern similar to that of *bombifrons* and *hammondii*, greenish or dark gray and with dorsolateral light spots or irregularly shaped stripes. Breeding seasons occur during the summer when rains are adequate.

Distribution.—West of the Colorado River in Utah and northern Arizona, and in the river valleys of the high plateaus that drain east into the Colorado River and west into the Great Basin. Primarily in the cold desert valleys of the Great Basin of western Utah, central and northern Nevada, southern Idaho, and Oregon, and in the Columbia River basin of western Idaho, southeastern Oregon, eastern Washington, and southern British Columbia.

Remarks.—The Colorado River appears to divide the ranges of *S. intermontana* from *S. hammondii* in Utah and northern Arizona. Tanner (1939) included San Juan County, Utah, in the range of *intermontana*. Specimens examined east of the river in southeastern Utah (Montezuma Creek, SE of Blanding, Utah) are *hammondii* and have the same skull characters as those examined from San Juan County in northwestern New Mexico. Indications are that the Colorado River and perhaps the desert areas along both sides have served as barriers to these species.

Populations west of the river from Kane County north to Uintah County show varying degrees in the development of the interorbitals. In all specimens examined there are two features that characterize these populations, and the species *intermontana*. First, the interorbitals are arched dorsally, producing a convex structure when viewed laterally. The interorbitals are without a distinct boss. Second, there are varying degrees of bone and associated connective tissues extending into the interorbital fontanelle. In all specimens examined the reduction in the size of the fontanelle is more apparent anteriorly, with the posterior part being reduced slowly and the last area to be closed. The series of figures show the skull structures from north to south in the environs of basins draining east into the Colorado River and west into the Great Basin (Fig. 5); although the basic skull characters are present, there is a north-to-south cline in which a progression of fontanelle closure is obvious.

Those specimens examined, from the Great Basin areas west of the Colorado River and from Idaho, all have the arched interorbitals and either a thickening of the interorbitals or thin extensions of bone into the fontanelle. In either case the size of the fontanelle is reduced and the dorsal aspect of the skull more massive when compared with the same structures in *hammondii*.

Material Examined

Spea bombifrons.—Arizona: Cochise Co., Chiricahua Mt, BYU 8932; Lupton, BYU 8829; Apache Co., Navajoland, Many Farms, LACM 127299. Kansas: Douglas Co., 2 mi NE Lawrence, KU 153450; Meade Co., Rexroad Ranch, KU 22145, 22170; Morton Co., Rolla, KU 7180; Rush Co., Nekoma, KU 35030. New Mexico: San Juan Co., 2 mi NW Blanco, UNM 2843–51; Valencia Co., UNM 37883, 37893. Chihuahua: Colonia Dublán, BYU 415; outskirts Cd. Chihuahua, BYU 10440–44; 13 mi E Rancho Flores Magon, BYU 13962–66.

Spea hammondii hammondii.—CALIFORNIA: San Joaquin Co., Corral Hollow Rd, UC 68255, 176016; Corral Hollow Rd (Hwy J–2) 5 mi W to 5 mi E Alameda–San Joaquin Co. line, UC 145191–92; Corral Hollow, 30 mi E San Joaquin Co. line, UC 145187; Corral Hollow Rd, KU 176016; Corral Hollow nr Livermore, BYU 37058; Madera Co., San Joaquin Range Expt. Station, UC 77040; San Joaquin Range, nr O'Neals, UC 64186, 77041–42; San Diego Co., San Diego, BYU 2141; Baja California Norte, El Rosario, BYU 34551; Punta Bunda, BYU 2761.

Spea hammondii multiplicata.—CHIHUAHUA: Chuhuichupa, BYU 14388–402, 14404–13, 15391–409; 11.1 mi NW Yepomera, UAZ 34818; 2 mi S Creel on rd to La Bufa, BYU 15598, 17081; Cerocouhui, BYU 15502–03. MORELOS: 3 km W Cuaulixco, KU 84890. NUEVO LEÓN: 33 km S San Roberto, KU 117350. OAXACA: 6 km SE Oaxaca, KU 117345; Mexico, San Juan Teotihuacan (the Citadel), BYU 13195–96.

Spea hammondii stagnalis.—NEW MEXICO: Eocene Plateau, northwest, USNM 8653, 25335 (cotypes); McKinley Co., 7 mi N 3.5 mi E Crownpoint, UNM 3236, 24141; Rio Arriba Co., 42 mi N Espanola (US Hwy 84), UNM 24401; 0.5 mi S Cuba (NW Hwy 197), UNM 24360; Sandoval Co., 7.2 mi NW Blanco, UNM 2843–47, 2849, 2850–51; San Juan Co., 17.6 mi N San Juan, McKinley Co. line, UNM 18957–62, 24132–40, 24150, 24155–56, 24160–61; 0.5 mi W Kirtland, UNM 47613–14. San Juan Co., 3 mi S Espanola, UNM 24371, UNM 38062–63 (no locality), 30 mi W Los Lunas, Hwy 6, UNM 15992, 25 mi W Los Lunas, UNM 15989, near Grants, KU 7183; Valencia Co., 1 mi E Rio Grande Gorge Bridge, UNM 13576–77; Taos Co., near Inscription Rock, KU 7177. ARIZONA: Apache Co., Navajoland, Many Farms, LACM 127298; Cochise Co., Chiricahua Mt, BYU 8839, 8939. TEXAS: Brewster Co., BYU 2767, KU 10276, Benton, BYU 2149, 2764. UTAH: San Juan Co., Montezuma Creek, BYU 18460–61. CHIHUAHUA: 12 mi SE Babicara, BYU 14453–67, 15571–80; 10 mi W San Francisco del Oro, BYU 15677; Colonia Dublan, BYU 415; 0.3–18.3 mi SE Madera, UAZ 34649–51, 34656–61, 34663–64, 34666–68, 35040; Yepomera, UAZ 34652–55, 34804–13; 3.8 mi SE Yepomera, UAZ 34814; 6.2–6.6 mi NW Yepomera, UAZ 34815–17, 35401; 2 mi S Santa Clara, MVZ 70622–45; 1 mi S 0.5 mi E Santa Clara, MVZ 72790; 5 mi N Cerro Campana, MVZ 72791; Ojo de Laguna, MVZ 72792; Arroyo Mesteno (Sierra del Nido), MVZ 72787–89. DURANGO: 18.8 mi N Cd. Durango, BYU 15513–27, 15835–37; 10 mi NE Cd. Durango, BYU 10436–39. SONORA: 3 mi (hwy rd) N Fronteras, UAZ 39069; 0.6 mi (Mex. Rd 2) E jct Janos-Cavarea and Agua Prieta Rds, UAZ 39065; 34.1 mi S Nogales, BYU 23990.

Spea intermontana.—ARIZONA: Coconino Co., Pleasant Valley, Kaibab Forest, BYU 45. CALIFORNIA: Mono Co., Hot Creek, S Mono Lake, BYU 21975–82, on Hwy 168 0–10 mi E jct with Hwy 295, UC 145204. IDAHO: Ada Co., Kuna Cave, BYU 44; Butte Co., A.E.C. Test Site, Arco, BYU 30221–25, 30338, 30341, 30651–76; Canyon Co., 45 mi S Nampa on Hwy 45, BYU, 40684–89; Fremont Co., Egin, BYU 8177. OREGON: Linn Co., Sweet Home, BYU 31440–44 + 18 untagged specimens. UTAH: Beaver Co., Beaver, BYU 12764–65; Wah Wah Mts, Pine Grove Canyon Reservoir, BYU 36924–27; Box Elder Co., Rossette, BYU 13037; Carbon Co., Helper, BYU 2055, 2058–63, 2070, 2073–74, 2800; Price, BYU 2169 + 30 tadpoles; Daggett Co., Bridgeport, BYU 14171–72, 14181; 2 mi S Linwood, BYU 14180. Duchesne Co., Duchesne, BYU 8085–87. Emery Co., Green River, BYU 47; 18 mi SW Green River, BYU 47, 787. Garfield Co., jct Boulder Creek–Escalante River, BYU 2017, 2022, 2263, 2772; 10 mi S Coyote Gulch, BYU 16679; 10 mi S Escalante, BYU 49, 50, 785; Henrieville, BYU 12921; 15 mi NW Hite, Hag Springs, BYU 16647, 22105; Pasy Lake, BYU 52; Steep Creek below road at Lakes, BYU 1956, 1958, 1968, 1970–71, 1973, 1975, 1977–79, 2768. Juab Co., 5 mi W Cherry Creek, BYU 9074–76 + 5 untagged specimens; Cherry Creek, BYU 9071; Ekker Ranch, W. Jericho, BYU 9422, 9431–36; Jericho Pond, BYU 9424, 9428–30, tadpoles no. 38382 with 33 specimens + 2 young toads; Playa Lake, 9 mi E Callao, BYU 14803–07, 14809. Kane Co., Crossing of the Fathers, BYU 14724, 14958, 16716; Grosvender Arch, BYU 41085–87; Navajo Wells, 14 mi W Kanab, BYU 23608–13 + 53 untagged specimens; Orderville, BYU 477, 1638, 1980, 2168; Paria River, BYU 12501; Willow Spring Tank, BYU 51, 55, 786, 788–89, 798–800, 8714. Millard Co., Flowell, BYU 23483–84, 10 mi S Gandy, BYU 46, 783–84; Salt Lake Co., Draper, BYU 23332–33. Sanpete Co., Indianola, BYU 2977. Tooele Co., Dog Area, Dugway Proving Grounds, BYU 14790–91, Government Creek, Dugway Proving Grounds, BYU 14789; Dugway Proving Grounds, 14801–10. Uintah Co., mouth of Brush creek, BYU 545. Utah Co., Cedar Valley sand dunes, 1 mi S Fairfield, BYU 2864; Orem, 400 S and U.P. Railroad, BYU 8340, 8342, 8344; Palmyra, BYU 23583, Provo (river bottoms), BYU 14801–02, Salem Pond, BYU 32074; Spanish Fork, BYU 23480. Wayne Co., Torrey, BYU 16557. Washington Co., Berry Springs, 3 mi W Hurricane, BYU 3720–21, 3732, 3736–38; Ivans Bench, BYU 9843, Ivans Reservoir, BYU 23505–49; Rockville, BYU 11315; St. George, BYU 2775, 8687; Terry's Ranch, BYU 12818; Zions Natl. Park, BYU 43, 780, 2773.

ACKNOWLEDGMENTS

I am grateful to Drs. George R. Zug and R. W. McDiarmid and the Smithsonian Institution (USNM) for the loan of two type specimens of *Spea stagnalis* Cope; Dr. Charles Lowe, University of Arizona (UAZ), for the loan of specimens, for suggestions as data were being assembled, and for reviews of the manuscript; Dr. H. L. Snell and the Museum of southwestern Biology, University of New Mexico (UNM) for the loan of specimens; Dr. W. E. Duellman and J. T. Collins, University of Kansas Museum of Natural History (KU), for the loan of 14 *Spea* skeletons; Dr. D. B. Wake, Museum of Vertebrate Zoology (MVZ), for the loan of 9 *Spea* skeletons; Dr. J. W. Wright, Los Angeles County Museum (LACM), for the loan of 2 skeletons; Dr. R. C. Drewes, California Academy of Sciences (CAS), and the M. L. Bean Life Science Museum (BYU) for the privilege of examining specimens; and Drs. Hobart M. Smith and Stephen L. Wood for reviewing the manuscript.

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VARIATIONS IN *THAMNOPHIS ELEGANS* WITH DESCRIPTIONS OF NEW SUBSPECIES

Wilmer W. Tanner[1] and Charles H. Lowe[2]

ABSTRACT.—Two new subspecies are described from the southern part of the distribution of *Thamnophis elegans*: *T. e. arizonae* from the Little Colorado River basin of Arizona and New Mexico and *T. e. vascotanneri* from the Upper Colorado River basin of Utah.

Few reptilian species in western North America occupy a geographical area as large and diverse as does *Thamnophis elegans*. Within this area Fitch (1983) listed six subspecies. Of these six, *T. e. vagrans* Baird & Girard (1853) is mapped as occurring in an area extending from southwestern Canada (Saskatchewan, Alberta, and British Columbia) southward in the high mountains and plateaus of the United States to Arizona, New Mexico, and Chihuahua, Mexico. Such a vast area includes a number of diverse basins including the Fraser River, Columbia River, headwaters of the Missouri River, Great Basin, Upper Colorado River basin, and smaller areas on the margins of some or all of these. It is not the intent of this study to report on populations from all of this area; only those in the eastern Great Basin, Upper Colorado basin of Utah, and the Little Colorado basin of Arizona are included.

Before examining the *Thamnophis elegans* populations, we discuss briefly some of the geological and climatic conditions that have involved these southern basins during recent geological times. The well-known distribution of *T. elegans* in its western high-mountain habitats of today was certainly not its primary situation during the recent ice age (see Wells and Jorgensen 1964, Van Devender 1977, Tanner 1978, Van Devender and Spaulding 1979, Morafka 1988). Other areas in North America, including the Mexican Plateau, were also similarly affected by the post-pluvial climatic events that induced degrees of isolation by environmental change and a reduction of available aquatic and mesic habitat (Taylor 1942).

For many years naturalists have recognized the uniqueness of populations inhabiting springs and streams in valleys that are separated by mountainous or desert barriers in the intermountain area of the western United States. This is true particularly of fishes in the Great Basin and many orders of aquatic insects as well as some reptiles. As Holocene desiccation advanced after the close of the recent ice age, many species primarily associated with mesic or aquatic valley habitats became confined to progressively smaller, more isolated aquatic or mesic areas and commonly at higher elevations.

In western North America—and particularly in Utah, Arizona, New Mexico, and northwestern Chihuahua—the advancing Holocene aridity not only affected those taxa associated directly with meadows and streams such as the garter snakes, but of course many other reptiles and mammals. Populations so involved often became confined to mesic mountain habitats at progressively higher elevations above wider expanses of developing arid and semiarid valleys and lower foothills below. Thus, as the pluvial period drew to a close and valleys and low ranges were progressively transformed during Holocene time into desert and desert-border habitats, *T. elegans*, including the "wandering" *vagrans* and other taxa that had previously been widespread in mesic valleys, became restricted to narrow habitats along permanent streams, at springs, in meadows and streams within the higher mountain ranges, and near the bases of these mountains.

The slow post-pluvial desiccation of the southern valleys in Utah and adjacent Arizona resulted in areas of desert that completely isolate animal populations in widely detached river valleys or basins. The deeper canyons, such as the Colorado and its southern tributaries, provided little productive streamside habitat, thus intensifying the isolation of riparian taxa. Two areas discussed below have been strongly affected by the restriction of habitat by the developing aridity. These are the Little Colorado valley of Arizona and the Upper Colorado River basin, including the areas both east and west of the river and north and south of the Book Cliffs in Utah and western Colorado. Between the San Juan River in southeastern Utah and the Little Colorado River in northeastern Arizona is an important arid and semiarid area with few aquatic habitats; it has been an effective barrier that continues to isolate populations to the north and south of it.

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In the Little Colorado River valley eastward from near Winslow to St. Johns, Arizona, and southward into the headwaters of the Gila River is a population isolated from the *elegans* population in southeastern Utah and possessing characteristics not found in other populations in either Utah or Chihuahua, Mexico. Garter snakes from this area are characterized in part by a wide middorsal stripe with few invading dark spots along its margins (Fig. 1). This racial distinction is in contrast to the population northward in southeastern Utah in which the dorsal stripe is completely obliterated in most and nearly obliterated in others by the numerous invading spots on each side of the dorsal stripe. The greatly increased size of the spots forms *dark bars across the dorsal stripe*, resulting in a series of dark and light spots rather than a dissected dorsal stripe; this pattern is accentuated in juveniles (Fig. 2, 3). Because of these distinctive color patterns, each population is readily differentiated from the subspecies *T. e. vagrans* in the eastern Great Basin of Utah and beyond, within which taxon they have been included in previous studies (Fitch 1983). We describe below the population in the Little Colorado basin.

Thamnophis elegans arizonae, n. subsp.

HOLOTYPE.—BYU 13358, an adult female taken in a marsh approximately 2 miles east of Joseph City, Navajo Co., Arizona, 20 April 1956, by W. W. Tanner.

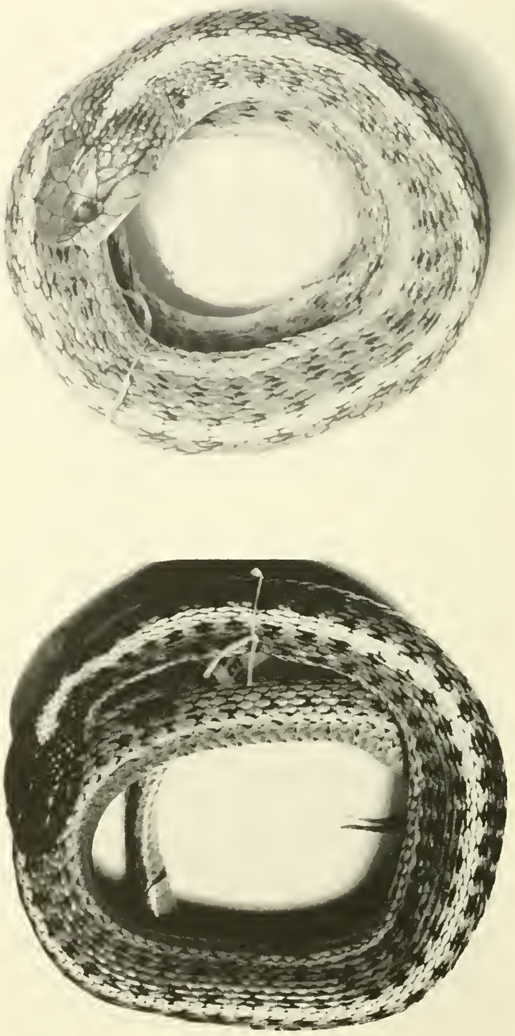

Fig. 1. *Thamnophis elegans arizonae:* top, BYU 13358; bottom, BYU 13249. Both from 2 mi E Joseph City, Navajo Co., Arizona.

PARATYPES.—ARIZONA: *Apache Co.:* UAZ 33528, Canyon de Chelly Natl. Mon., upper canyon del Muerto, 2 mi S and 3.7 mi W St. Ann Church (Tsaile); UAZ 33635–36, Canyon de Chelly Natl. Mon., upper canyon del Muerto, below Tsaile Lake Dam; UAZ 35918, 4.3 mi (on U.S. 180) W St. Johns; UAZ 37458, 37460–67, Crescent Lake, ca 21 mi (rd) SW Eager; UAZ 37470, Basin Lake, ca 22 mi (rd) SW Eager; UAZ 39493, 4.3 mi (on U.S. Highway 666) S St. Johns. *Navajo Co.:* BYU 12786–91 topotypes; BYU 13355–57, 4 mi E Shumway; UAZ 41861, 1 mi S Pinetop. NEW

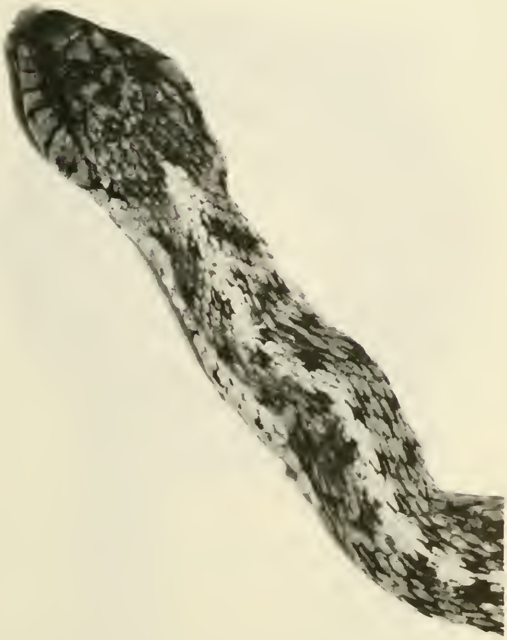

Fig 2. *Thamnophis elegans arizonae:* UAZ 3943, 4.5 mi S St. Johns, Apache Co., Arizona.

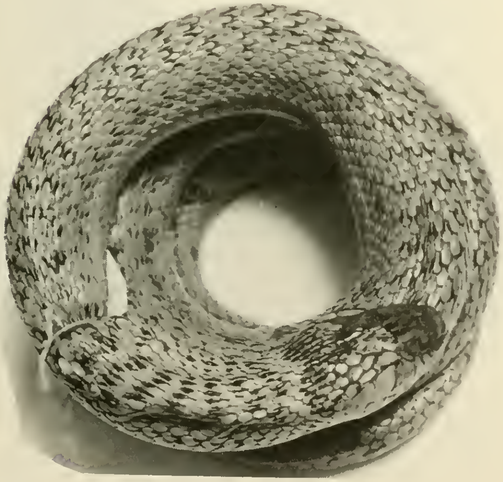

Fig. 3. *Thamnophis elegans vascotanneri:* BYU 10245, junction of Boulger Creek and Huntington River (now submerged by Electric Lake), Emery Co., Utah.

MEXICO: *Catron Co.:* UAZ 36370, Berland Lake, 17.4 mi SW U.S. 666 and ca 10 mi S Newcomb; UAZ 43145, Romero Creek, S of road crossing 10.4 mi NW Luna; UAZ 43141–42, Tularosa Creek S hwy crossing 13.1 mi (rd) E Reserve; UAZ 43196, Jenkins Creek at ca 8,600 ft W Spier Lake Basin. *McKinley Co.:* UAZ 36370, Berland Lake, 17.4 mi SW U.S. 666 and ca 10 mi S Newcomb; UAZ 36372, Marchy Lake, 15.7 mi SE U.S. 666 and 10 mi S Newcomb.

DIAGNOSIS.—Characterized by a broad middorsal stripe, usually 2–3 scales wide and with small marginal dark spots not or only slightly invading the dorsal stripe, stripe expanded above the angle of the jaws (Fig. 1). Ventrals 150–174, male 163–174 (166.4), female 156–165 (160.6); caudals, 68–92, male 80–92 (86.4), female 68–84(75.0).

DESCRIPTION OF HOLOTYPE.—An adult female with a total length of 833 mm, tail 197 mm and 23.7% of total length; head length, snout to end of parietals, 21.6 mm; head width, 20.2 mm; dorsal scales in 21-21-17 rows, ventrals 162, caudals 77, supralabials 8-8, infralabials 10-10, preoculars 2-3, postoculars 3-4, loreal 1-1, temporals 1+2+3.

In the color pattern the light-colored middorsal stripe occupies three scale rows. Small spots along its margins do not invade the stripe; midlateral dark spots are larger than those near the stripe, are irregular in shape, and have a fragmented appearance. Temporal spots are slightly darkened and divided by a single row of light scales extending from the dorsal stripe to the parietals. A lateral stripe on scale rows 2–3 is only slightly lighter than the first scale row; the first scale row is of the same light gray color as the ventrals, with a few small dark spots scattered irregularly along its margins (Fig. 1).

REMARKS.—There is little variation in the scale patterns. In the females the ventrals vary by only nine scales in a series of 20 specimens, and the scale rows are constantly 21-21-17. The oculars in the type at 2-3 and 3-4 are not normal; all others in the type series have 1-1 preoculars, but three other females have 3-4 postoculars. In the subspecies *vagrans* the small dark spots indent the margins of the dorsal stripe or dissect it; in *arizonae* these spots remain at the margin with few indentations.

A comparison of *T. e. arizonae* with specimens from western Chihuahua, Mexico (*T. e. errans*), indicates a similar enlargement of the middorsal light stripe posterior to the parietals. Posterior to the enlarged area the stripe

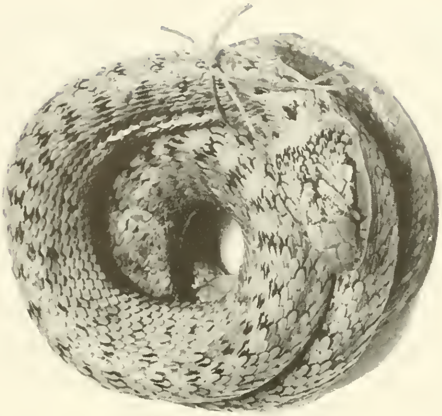

Fig. 4. *Thamnophis elegans vascotanneri*: BYU 544, Bryce Canyon Nat. Park, Garfield Co., Utah.

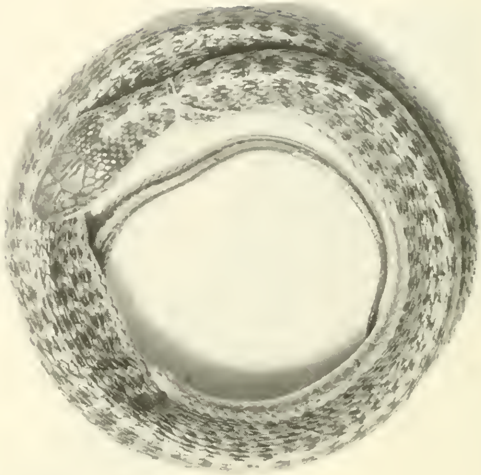

Fig. 5. *Thamnophis elegans vagrans*: BYU 16618, south side of Provo Airport, Utah Co., Utah.

narrows to involve only the middorsal scale row, forming a narrow stripe without the indenting (invading) of the stripe by dark spots along its margins (Fig. 4). Also in *errans* there are undulating dark bars on the body lateral to the dorsal stripe. These and other color pattern variables strongly indicate that these now widely separated populations (*vascotanneri*, *arizonae*, and *errans*) were, before the subcontinental desiccation, a single, widespread, interconnected series of populations. Only through isolation have color and scale patterns been modified. Specimens from New Mexico and those south of the Mogollon Rim in Arizona show characters that relate them to *errans*. (For additional information concerning *errans* see Tanner 1959, 1985 [1986], and Webb 1976.)

Thamnophis elegans vascotanneri, n. subsp.

Upper Basin Garter Snake

HOLOTYPE.—BYU 10245, an adult female taken at the junction of Boulger Creek and Huntington River, Emery Co., Utah, 18 June 1950, by Helen B. and Wilmer W. Tanner.

PARATYPES.—UTAH: *Carbon Co.*: BYU 2790, Price; BYU 23033, 1 mi N Price. *Daggett Co.*: BYU 205, 8834, Sheep Creek; BYU 511, 1608, 1610, Elk Park; BYU 14173, 5 mi E Clay Basin Station. *Duchesne Co.*: BYU 179, Neola; BYU 188, Duchesne; BYU 4058, 4078–82, Ioka. *Garfield Co.*: BYU 169, 1015–21, Escalante; BYU 170, 1022–24, 1029–30, 1859–62, 8318–20, Steep Creek, Boulder Mt; BYU 171, 1925–27, 1936–37, Boulder; BYU 183, 1846, 1848–49, 1855–56, 1873, Posy Lake, Boulder Mt; BYU 664, Cyclone Lake, Boulder Mt; BYU 668, 1874–75, 2255, 2257–58, Escalante River at junction of Calf Creek; BYU 2131–32, 2740, 22473, Tropic; BYU 21708, Indian Creek (Moki area). *Grand Co.*: BYU 190, 1052, Green River; BYU 197, 1056, Moab; BYU 260, 1174, Blue Lake, LaSal Mts. *Kane Co.*: BYU 682–83, 1940–41, Orderville; BYU 8324, 11 mi W Kanab; BYU 30433, Findlay Ranch, 40 mi E Kanab. *San Juan Co.*: BYU 194, LaSal; BYU 196, LaSal Ranger Station; BYU 200, Bears Ears, Elk Ridge; BYU 11309, Redd Ranch, 3 mi W LaSal; BYU 13789–91, Kingalea Ranger Station, Elk Ridge. *Uintah Co.*: BYU 518, mouth of Brush Creek; BYU 11267, Tridell. *Wayne Co.*: BYU 176, 1028, Notom; BYU 663, 1857–58, Torrey; BYU 667, 1865–72, 3694, Fruita.

DIAGNOSIS.—Characterized by the absence or modification of the middorsal stripe by dark cross bars, leaving in some specimens only a series of light spots in the dorsal area. This is in contrast to the broad stripe in *arizonae* (Fig. 1) and the irregular, indented stripe in typical *vagrans* (Fig. 5). Ventrals 158–180, male 164–180 (171.5), female 158–170 (168.0); subcaudals 64–93, male 76–93 (85.8), female 64–85 (75.6).

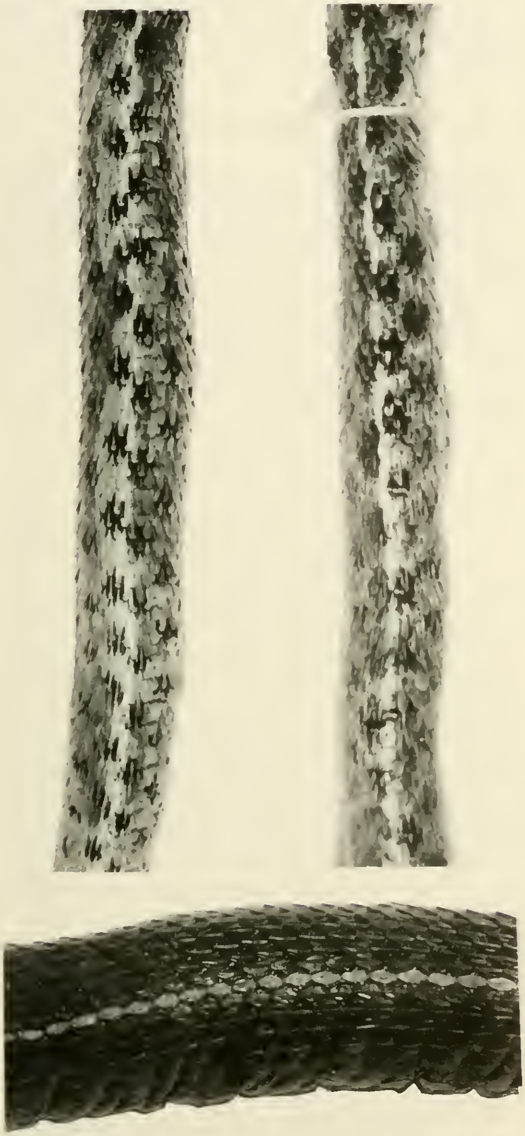

Fig. 6. *Thamnophis elegans vagrans:* top left and right, BYU 16618–16619, showing the irregular, zigzag dorsal stripe; bottom, dorsal view of *Thamnophis elegans errans*, BYU 17076, with a single scale row in the dorsal stripe, 2 mi S Creel, Chihuahua, Mexico.

Description of Holotype.—An adult female with a total length of 983 mm, tail 186 mm with tip missing; head length 22.5 mm, head width 21.1 mm; dorsal scales 21-21-17 with the reduction to 17 at ventrals 165–168; ventrals 168, subcaudals 64, supralabials 8-8, infralabials 10-10, preoculars 1-1, postoculars 4-4, loreal 1-1, temporals 1+2+3.

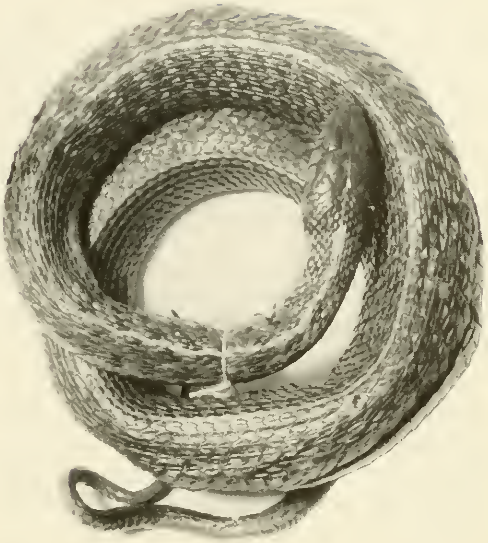

Fig. 7. *Thamnophis elegans errans:* BYU 17076, 2 mi S Creel, Chihuahua, Mexico.

The middorsal stripe is absent, with irregular dark cross bars spaced regularly on the dorsal and lateral surface (above lateral stripe) of the body. Ground color of body and tail a lead grey with the dark bars showing prominently, temporal spots joined medially and the same color as the dark body spots. Lateral stripe on rows 2–3, but not prominent, having only a lighter shade of grey than that of the body; ventrals a uniform dark grey; few widely spaced, small dark spots on the edges of ventrals and the first row of scales; head scales a light brown laterally and grey dorsally (Fig. 2).

Remarks.—The determination by Fox (1948) that *T. ordinoides* and *T. elegans* were distinct species gave stability to the systematics of the *Thamnophis elegans* complex of subspecies. Furthermore, his data suggest also that *T. elegans* was, during and perhaps previous to the last pluvial period, a widespread and relatively uniform series of populations within the valleys of the intermountain west of North America. With the slow desiccation of the last 10,000 to 20,000 years, the extensive distribution once available to *T. elegans* has been dissected and constricted into smaller areas, with reduction or elimination of a contact between subspecies and local populations. Examples of this are seen in *T. e. errans* of Chihuahua, which is separated from the Arizona–New Mexico *T. e. arizonae* by a wide expanse of arid desert and semiarid desert grassland, and is in turn similarly isolated from the *elegans* in the Upper Colorado River basin. In these subspecies, as well as *T. e. vagrans* and others, both the scale and color patterns have been significantly modified. Geographic isolation and a slowly changing habitat in conjunction with genetic isolation by distance are undoubtedly responsible for the observed changes in scale and color patterns.

When the type of *T. e. vascotanneri* was collected, the senior author did not immediately recognize it as an *elegans* and certainly not the same as the *e. vagrans* specimens seen in the Great Basin of western Utah. If the type locality of *T. e. vagrans* is in southwestern Utah (it is probably between Utah and Iron counties), then the more typical *T. e. vagrans* has a color pattern in which a yellowish middorsal stripe is present and has on each side small dark spots that invade each edge. The invading, alternating spots on each side form a zigzag stripe (Fig 5). As indicated above, it is not our intention to report here on the entire series of populations of *elegans vagrans*. Those seen from the Great Basin, the Snake River, and the Columbia River basin of western Washington appear to have the basic characteristics of *T. e. vagrans*.

ETYMOLOGY.—The name *vascotanneri* honors the late Dr. Vasco M. Tanner. In the fall of 1925, Dr. Tanner arrived at BYU as chairman of the Department of Zoology, a position he held for 33 years. He had just completed his doctoral degree at Stanford University and, having been associated with David Star Jordan, was enthusiastic about the possibilities of natural history in Utah and the Great Basin. During the next few summers he took field trips to several parts of Utah; on one of these in southeastern Utah he collected perhaps some of the first reptile specimens of this subspecies. The low museum numbers for these specimens indicate the beginning of the collection now housed in the M. L. Bean Life Science Museum. It is both fitting and our privilege to name this *elegans* subspecies in his honor.

ACKNOWLEDGMENTS

We are indebted to the M. L. Bean Museum for the privilege of examining specimens in its herpetological collection (BYU) and to the University of Arizona (UAZ) for additional material examined from its herpetological collection. This manuscript was reviewed by Drs. Hobart M. Smith and S. L. Wood. The photographs were prepared by Mr. Mark Philbrick.

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ON THE STRUCTURE AND FUNCTION OF WHITE-TAILED PRAIRIE DOG BURROWS

James A. Burns[1], Dennis L. Flath[2], and Tim W. Clark[3]

ABSTRACT.—The architecture of burrows of the white-tailed prairie dog (*Cynomys leucurus*) is poorly known. For this reason and for comparative purposes, one recently active burrow of this species was excavated in southern Montana; the detailed methodology is described. Data were compiled on the dimensions of the 29.3 m of excavated passages, and interpretations of several features are discussed. A "turning bay," sleeping quarters, two hibernacula, and a maternity area are described, the last feature for the first time in print. In addition, we report *Cynomys* using their teeth to dig, also for the first time. Further, an inadvertent remodeling of the burrows is ascribed to normal animal traffic and appears to confirm a prediction based on late Pleistocene fossil burrows in Alberta.

The white-tailed prairie dog (*Cynomys leucurus:* Rodentia: Mammalia) may spend almost two-thirds of its life underground (Clark et al. 1971) in laboriously constructed burrows. Burrows provide shelter from inclement weather and predators, and a peaceful place for bearing and rearing young; they are also important to the social structure of the colony (King 1955, 1984). Research on subterranean architecture has concentrated on other *Cynomys* spp. For *C. ludovicianus*, tunnel schematics (Merriam 1901, Scheffer 1937, Wilcomb 1954) and tabular data (Sheets et al. 1971, Whitehead 1927) are available, and for *C. gunnisoni,* schematics (Foster 1924, Longhurst 1944). Clark (1971, 1977) provided the only *C. leucurus* schematics, and these are of only one tunnel and part of a second.

This paper discusses the excavation of one *C. leucurus* burrow in southern Montana, at the northern edge of the range for this species (Flath 1979). It was not a complete system but rather what we could excavate in five days. One of us had recently excavated fossil *Cynomys* burrows in southern Alberta, Canada (Burns and McGillivray 1989), and to facilitate comparison of the fossil and Recent burrows, we employed similar mapping techniques. The fossil burrows are to be described elsewhere (Burns and Young, in preparation).

STUDY AREA

The burrow chosen for study is located in Sec. 31, T9S, R27E, Carbon County, Montana (see Flath 1979). A Carbon County specimen of *C. leucurus* (U.S. National Museum #67369) collected in 1894 attests to the lengthy occupation of the region (R. D. Fisher, personal communication, 1987). Annual precipitation in this northernmost portion of the Bighorn Basin is 15–23 cm (Flath and Paulick 1979). Vegetative ground cover is 40–50%, consisting largely of big sagebrush (*Artemisia tridentata*), saltbush (*Atriplex nuttallii*), and a limited variety of forb species, but little graminoid forage. Although rain is scarce, erosion channels in the bare soil indicate that high rates of erosion can occur with occasional summer rains.

The soil is very hard and is characterized as a dense clay-clayey-saline upland soil (Parker et al. 1975). On the ground and throughout the subsurface soil are vast numbers of fragmentary shells of an undetermined species of Jurassic pelecypod mollusc, *Gryphaea*. These were likely redeposited from Jurassic strata in the Bighorn Mountains during the formation of an early Holocene playa lake in the basin.

METHODS

Flath and Paulick (1979) identified complex (= maternity) and simple burrow mounds. The mound chosen to begin the excavation was classified as simple in this scheme: dome-shaped and featuring a single opening. The moderately pitched tunnel was first probed with a 2.4-m flexible plumber's cable. A rope-filled canvas sack was pushed into the tunnel as far as possible to keep the burrow free of loosened earth. A backhoe (Case 580E) with a 0.25-yd^3 (0.19-m^3) bucket was used to remove earth from the surface in small portions. The dig was cleared at appropriate intervals to determine the direction of the tunnel and to measure its dimensions.

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Planar coordinates were measured at flagged and numbered "survey points" along the tunnels. Elevations were determined relative to a datum stake with a surveying transit. All measurements were tied into a grid system constructed on magnetic north and laid out in a pattern of squares 5 m on a side. Horizontal position of points was determined from angular coordinates measured from two designated corner-posts within the corresponding 5-meter square using a plumb bob to position the tape measures over the point. In addition to the point coordinates, the vertical and transverse diameters of the tunnel at those points were recorded. A note was made of the portions of the tunnel that were plugged and of the composition of the plugs. After clearing a plug almost 4 m beyond the mouth of the first mound, we identified the second entrance by using a smoke bomb (cf. Stromberg 1975).

RESULTS

The openings of the selected burrow, on mounds A and B, were both of the dome type (cf. King 1955). The shortest distance along the tunnels between openings was 16.5 m. We mapped an additional 12.8 m of lateral tunnels; four other leads could not be completed due to lack of time. Plan and perspective views are given in Figures 1 and 2. At point 4 (hereafter, pt. = point), 13 cm below surface and 65 cm from the opening in mound A, was a two-part chamber similar to Scheffer's (1937) "turning bay." A lower exit led down to pt. 7, where a north-south tunnel intersected. The main tunnel was indistinguishable from the cross-tunnel, as both were plugged with similar plant-rich material. It is uncertain whether the cross-tunnel fortuitously intersected, or was part of, the main system. Lack of time prevented pursuit of the cross-tunnel beyond pt. 10 (Fig. 1).

The main tunnel proceeded west. At pt. 13, a major side-tunnel that branched southward was completely plugged with earth, plant matter, and feces. At pts. 35 and 42, two chambers of modified globular and globular shape, respectively, were filled with semifresh plant matter, apparently the roots and shredded bark of *Artemisia*. The chamber at pt. 42 was 24 cm high and 23 cm across and was filled with more than 3 L of plant stuffing but no feces. The side-tunnel ended at pt. 45 in a narrow cul-de-sac 6 cm in width. A chamber of an independent burrow was located above this terminus (Fig. 1). An adult *Cynomys* humerus was found at pt. 39 in the chamber and a tibia and metatarsal at pt. 40. (Only one other bone was found below ground, a *Cynomys* metacarpal at pt. 10). The upper burrow was plugged with old plant matter.

The main tunnel made a sharp northward bend at pt. 16 and continued to an intersection at pt. 19. The area immediately to the north was enlarged but not to full chamber dimensions. Two tunnels branched off at pts. 20 and 21, but time did not allow pursuit of them. The main route led to the bottom, at pt. 30, of an inclined shaft, which then led up to the opening on mound B.

To the north of pt. 30 the entire complex was plugged with earth and feces, including numerous 5-mm-long juvenile pellets. Three tunnels branched off the complex at pts. 54, 49, and 55. The complex contained three subchambers, all of which were clearly modified by shallow, accessory diggings. The tunnel from pt. 55 to pt. 65 and beyond could not be followed due to lack of time. Pts. 49 and 55 led to a common tunnel that terminated in a vertical shaft at pt. 57. The top of the shaft was not seen to reach ground surface anywhere during excavation and is thought to have been a blind vertical terminus. Pts. 54 and 67 were ends of a common tunnel that featured another vertical terminus, at pt. 69. This was carefully uncovered during excavation and could not have reached the surface.

In summary, the system as far as it was excavated, consisted of a 16.5-m-long tunnel connecting mounds A and B. The straight-line distance between mound openings was 11.3 m. The two mounds were simple domes with one opening each. The main tunnel had at least five side-branches, only one of which was completely dug; total length of excavated tunnels was 29.3 m. Three irregular and two globe-shaped structures were defined. One area in the northwest featured a moderately

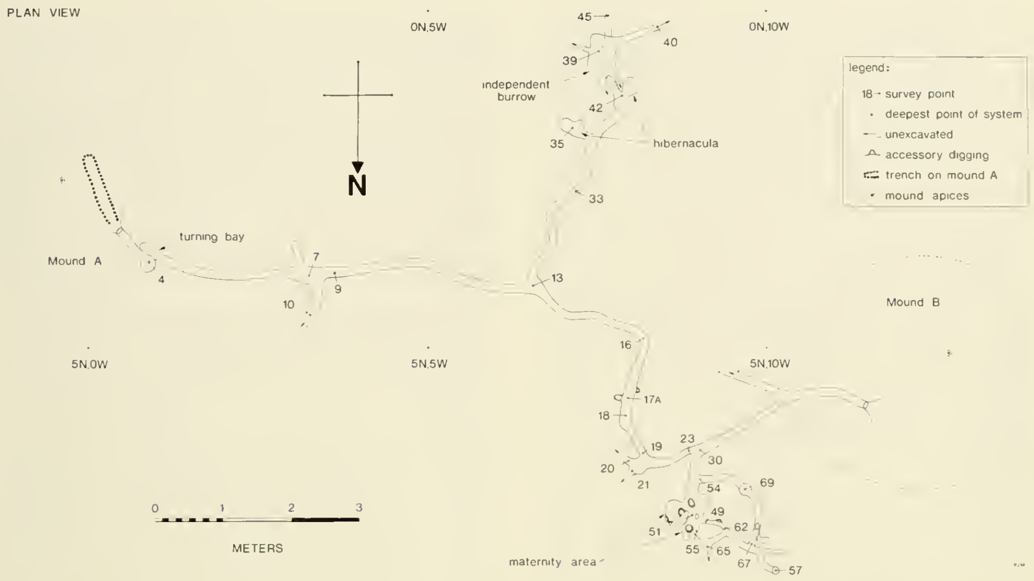
PLAN VIEW
0N,5W
45
40
0N,10W
39
independent burrow
42
35
hibernacula
33
N
legend:
18 survey point
deepest point of system
unexcavated
accessory digging
trench on mound A
mound apices
turning bay
Mound A
4
7
9
10
13
Mound B
16
5N,0W
5N,5W
5N,10W
17A
18
19
20
21
23
30
54
69
49
51
62
55
65
67
57
maternity area
0
1
2
3
METERS

Fig. 1. Plan map of the burrow system. Numbers refer to the survey points mentioned in the text. Arrows indicate leads that were left unexcavated. The unusual orientation of the north arrow was suggested by Figure 2, which is the optimal orientation for appreciating the features of the burrow system.

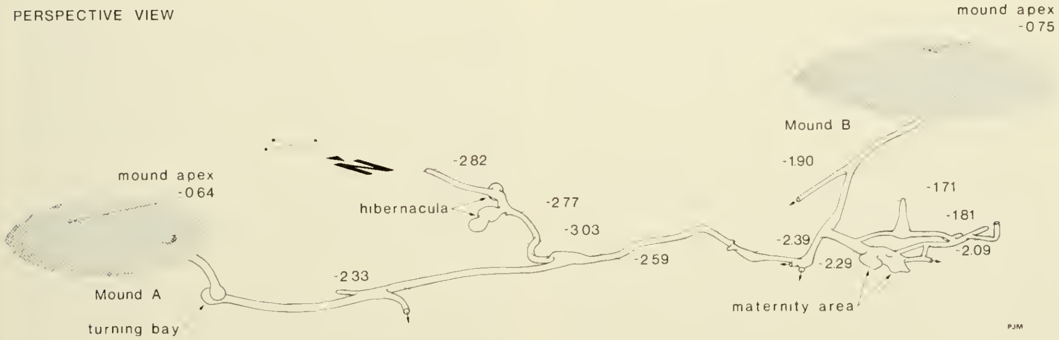
PERSPECTIVE VIEW
mound apex
-0.75
Mound B
-1.90
-1.71
-1.81
-2.09
-2.39
-2.29
maternity area
-2.82
hibernacula
-2.77
-3.03
-2.59
mound apex
-0.64
-2.33
Mound A
turning bay
PJM

Fig. 2. Perspective view of the burrow system. Negative values accompanying hash marks on the burrow are the elevations below a common datum stake.

complex network of tunnels and interconnections. The greatest depth of the system was 2.0 m below surface, at pt. 33 on the south side-branch. Average vertical and transverse diameters of tunnels were both 10–11 cm. Plugging was extensive throughout.

Discussion

Clark (1971, 1977) noted, based on available data at that time, that there were few if any criteria that distinguish the burrows of white-tailed and black-tailed prairie dogs. The results of the present study do not alter that conclusion but do include some worthy observations.

Tunnel plugging is a notable feature of prairie dog burrows. The purpose of the plugging is variously ascribed to a need for altering tunnel systems (Wilcomb 1954), to sanitary reasons, such as burying dead kin (Smith 1958), to protection from ferret predation (Henderson et al. 1969, Clark et al. 1984, Martin et al. 1984), to keeping winter food moist (Jillson 1871). The results of these studies are not always comparable, as some deal with artificial situations and some deal only with plugs at mound entrances. In the present study the only unplugged portion of the system extended from the opening on mound B eastward along the main tunnel to pt. 9, just west of the cross-tunnel. However, one intriguing feature of the system was that the opening on mound B was partially plugged with slopewash off the mound, resulting from heavy rains in the preceding month or two. Although not wholly occluded, the tunnel was impassable for a prairie dog. The side-branches, at pts. 7, 13, 20, 21, and 23, were occluded with richly organic materials. It is unlikely that the plugging observed near mound A was a protective measure because the cross-tunnel was similarly blocked; there was likely no hibernant beyond pt. 10. The southerly side-branch from pt. 13 to its terminus was entirely blocked, and yet near-fresh, unfouled nest material filled the globular chambers; at pt. 13 itself some recent (bright green interior) fecal pellets were noted, but the remainder of the plug was composed of old, dried pellets, plant matter, and some earth. Likewise, at pts. 20 and 21, old, dried organic plugs were present, and the multi-chambered area at pt. 51 was also filled with old plug material.

It seems that plugging was an effort to remodel. Longhurst (1944) suggested that earth from deeper, second-year passageways was packed into shallow, first-year tunnels, thus economizing on the effort to move it to the surface. Plugging for the purpose of underground food storage (as in Jillson's [1871] experiment) was not corroborated by the present study or others (Scheffer 1937, Longhurst 1944). Free-ranging prairie dogs do not store food below ground.

It may be that our system had been abandoned or that the hibernant was located beyond pt. 20 or 21. The latter option is less likely because plugs in these openings were tightly packed as if from the "near" side. As the prairie dogs were in hibernation in early October when we undertook the study, there was no way to know if the burrow was inhabited or not, short of exhuming an animal. The only signs of activity were the fresh pellets at pt. 13 and relatively fresh-looking "trench" on the surface of mound A (Fig. 1). The trench was worked from above as it did not reach into the lumen of the tunnel. Its purpose is unknown.

To date no studies have identified maternity areas within burrow systems. Flath and Paulick (1979) identified maternity systems based on observations of juvenile play groups frequenting certain mounds. Further, they identified 98% of these systems as having juvenile "accessory digging" in the entrance mounds.

Our mounds were not typical of such maternity burrows. Yet one area in the northwest portion of the system appears to have served a maternity function. The irregular chamber noted above, at pt. 51, with its subchambers, "grassy" nesting material, accessory diggings, and myriad small pellets, is a likely center of maternal/juvenile activity. Several other accessory diggings were noted, at pt. 17A (associated with a possible nest centered on pt. 18) and near pt. 62, just west of the maternity area. This is believed to be the first description of an underground maternity area.

Cynomys ludovicianus, *C. leucurus*, and *C. gunnisoni* can, and do, hibernate (Bakko and Nahorniak 1986, Harlow and Menkens 1986, Rayor et al. 1987); whitetails appear to be obligate hibernators, but blacktails are more variable in this. Nevertheless, the nature of the hibernaculum has never been described because torpid prairie dogs in the wild have never been reported.

The two globular chambers at pts. 35 and 42 may represent hibernacula. They were maximally distant from either mound opening; they were full of unfouled, shredded nesting material; and they do resemble in these features the hibernacula of the Columbian ground squirrel, *Spermophilus columbianus* (Shaw 1925; Burns, personal observations). Although proof requires finding torpid prairie dogs *in hibernaculo*, it is important to distinguish among hibernacula, maternity chambers, and normal sleeping quarters. It is not necessary that all systems possess all three features, but in the current study it seems to be so. The maternal and hibernacular sites are tentatively described above. Further, a widening in the tunnel, at pt. 18, to 18 cm wide may have functioned as sleeping quarters. Wilcomb (1954) encountered numerous such widenings in his study of 14 blacktail burrow systems.

Another feature of this burrow system was the occurrence of two vertical termini at pts. 57 and 69. Similar vertical "blind alleys" have been described in the popular literature as refuges from flooding. Foster (1924) reported casual observations of ranchers who saw a colony inundated for several hours and who claim no subsequent reduction in the prairie dog population. Upon excavation of a burrow, Foster noted several of the vertical termini and proposed the refuge hypothesis. Such a construction might work in the clayey soil of Carbon County, Montana, but only if enough rain fell to test it.

The terminus at pt. 69, 12 cm in mean diameter, extended up 39 cm to a blunt end above the roof of the underlying burrow. Surprisingly, the inner surface of the tube was riddled with the paired, linear gouges of *Cynomys* incisor teeth (Fig. 3A, B). The U-shaped cross sections of the gouges indicate the use of *lower* incisors for the digging. There is a divergence toward the end of the stroke in several of the paired gouges (Fig. 3C), made possible because the mental (mandibular) symphysis is flexible; no such flexibility exists between the premaxillae. The divergence opens upward, indicating motion from bottom to top. In at least 15 instances upper incisors were used to anchor the head in the earth while the lower jaw was being drawn upward and forward. Short, flat impressions of paired upper incisors are visible in these instances a few millimeters above the end of the lowers' stroke (Fig. 3D).

Some burrowing rodents (e.g., Geomyidae; Bathyergidae; Muridae: Spalacinae, Tachyoryctinae; some extinct Castoridae) normally use their teeth to dig (Martin and Bennett 1977, Vaughan 1978). For this they possess some or all of the following features: procumbent upper incisors, lips that prevent loose earth from entering the mouth, and horny nose pads that prevent abrasion on the nose (Martin and Bennett 1977, Vaughan 1978). It is to be noted that all of these species use their upper incisors; our *Cynomys* used their lowers. In any case, prairie dogs are ill adapted to digging with their teeth.

The Carbon County whitetails must have been desperate. The hard earth forced the digging teeth apart and in so doing would have stretched the gingiva painfully; the teeth must have been worn very rapidly, and the lips and nose probably suffered horribly from abrasion. It is difficult to imagine this self-mutilation unless they were in mortal danger. It is unlikely that a predator was threatening, because time would not have permitted such extensive digging. Perhaps there is an explanation in P. J. Young's (1988) observations of radio-tagged *Spermophilus columbianus* emerging from hibernation. He reported that the squirrels did not return to the surface by unplugging existing passages, and the evidence in the ground suggested that new tunnels were excavated straight to the surface from the hibernaculum. If the prairie dogs were emerging from torpor and digging their way out, there must have been a pressing need (hunger?) to get to the surface. Although Foster's (1924) explanation for vertical termini is unproven, it suggests an alternative for our site. Slopewash off mound B, presumably caused by flash flooding, had largely occluded the passage from the mouth down to pt. 30, as noted earlier. It could be that fear of drowning, with no negotiable exit, forced the attempt to burrow straight up, and with some alacrity.

Wilcomb (1954) noted blacktails using claws in the construction of tunnels in crumbly clay-loam soil. Under captive conditions, *C. gunnisoni* was observed using its front feet (i.e., claws) to burrow (Longhurst 1944). The present study is the first, to our knowledge, in which *Cynomys* has been shown to dig with teeth.

Loose soil on burrow floors is expected. Its depth is variable, from 0.5 cm (Wilcomb 1954) to as much as 5 cm (Clark 1971, 1977). Our study revealed the floors to be bare or slightly blanketed. However, in cross sections cut well below the lumina of the tunnels, dark stains traced out vague, semicircular outlines (Fig. 4). The dark subfloor soil was sometimes pasty in texture and, though organic, contained only grossly recognizable material (feces, plant stems, etc.). Survey flags could be driven into the floors easily, whereas the enclosing matrix was much too hard. This feature was predicted to occur in the modern context because it is well developed in the Pleistocene burrows of southern Alberta (Burns and Young, in preparation). Constructed in uncemented sands of Miocene age, the in-filled fossil burrows with normal 13–15-cm diameters show cross sections with vertical heights of up to 80 cm.

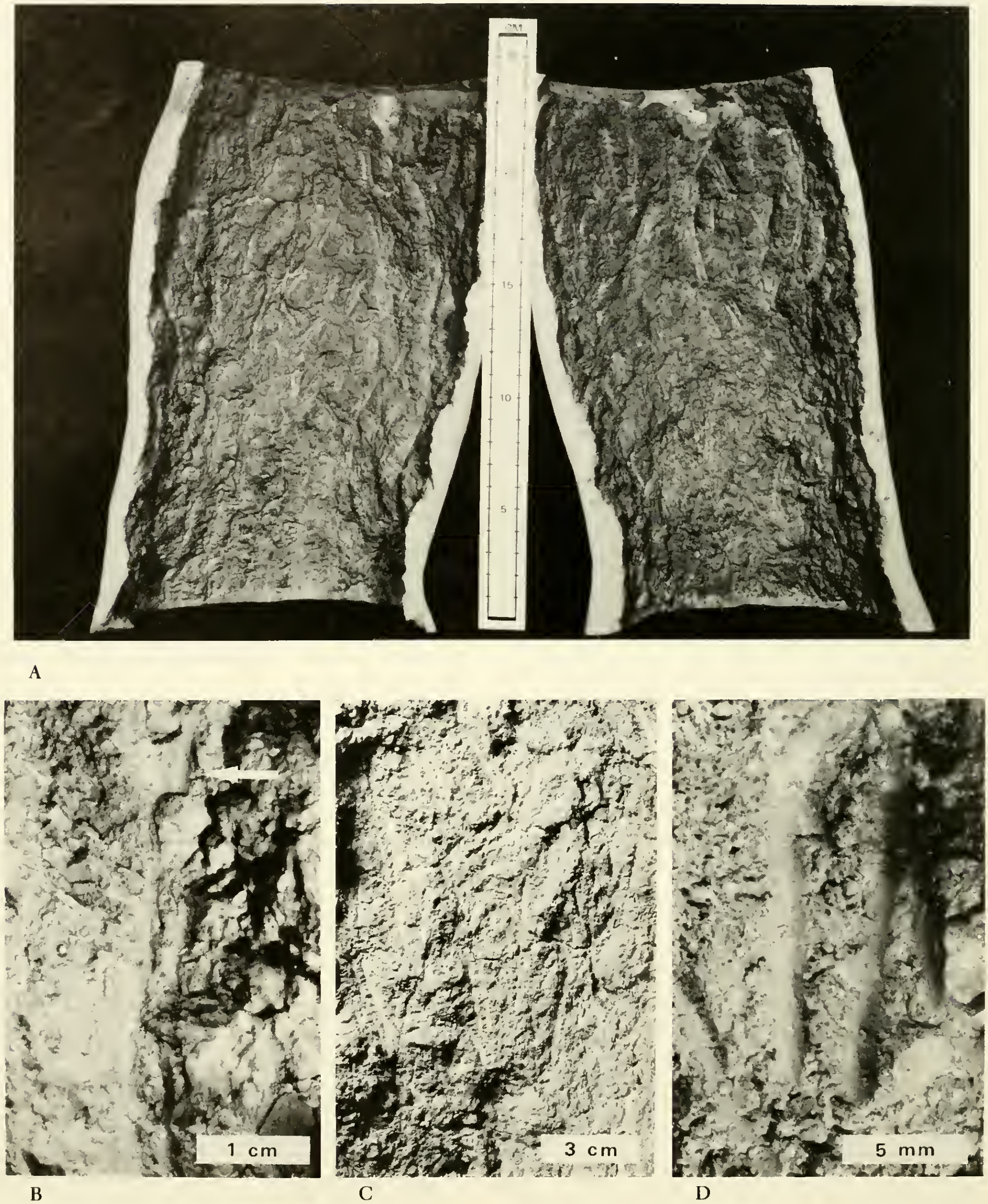

Fig. 3. Evidence of tunneling by *Cynomys leucurus* using the teeth: A, resin cast produced from the section of vertical tunnel at pt. 69; B, detail of a portion of the cast showing a number of the gouges produced mostly by the lower incisors; C, example of the divergence of the tooth gouges; ligaments of the mental symphysis were stretched as the jaw was drawn through the hard earth; D, example of the use of the upper incisors (arrow) to anchor the head while the mandible is adducted in the digging stroke.

One may postulate that, as the animals pass through the tunnels, they rub matrix from the walls and roof. The detritus falls down, becomes incorporated with scattered organic waste, and is then compacted by the traffic. As time passes the tunnel is remodeled. In effect, the tunnel "migrates" upward through the soil profile. Can such a scenario be taken

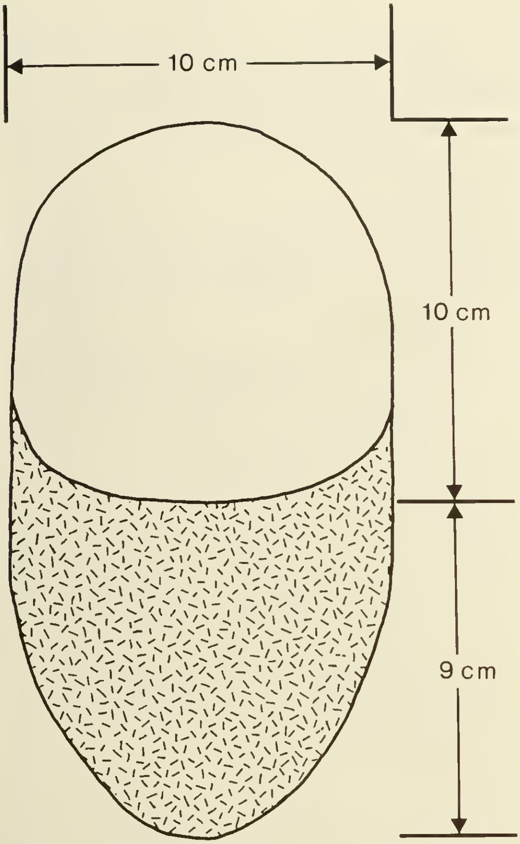

Fig. 4. Schematic of the tunnel profile at pt. 54. Typical of many loci in the system, this shows a patent passageway above a trace of the former passage. The process of upward "migration" of the passage is explained in the text.

seriously? Given that the soils are very hard, can casual contact promote remodeling? It is eminently possible given time. Although the age of this burrow is unknown, the colony is at least 93 years old. If economy of effort is a factor in the construction of burrows in the unyielding soil of this arid, scantily vegetated environment, then a burrow may be inhabited for several years at least. The resulting traffic of years could produce the alterations.

ACKNOWLEDGMENTS

The assistance of Mr. Dan Bricco, Montana Bureau of Land Management Office, Miles City, is gratefully acknowledged. Our lodgings and the use of a backhoe with operator were provided through his aid. Operator Ken Hanify was ever cheerful and patient with our unusual requests. Assistance in the field by Peter Milot, Jr., paleontology technician, Provincial Museum of Alberta, is appreciated; he also drew the figures, made the photographs, and offered insights on the dig. David Genter, The Nature Conservancy, Helena, Montana, lent a valued helping hand. Dr. Paul Johnston, Tyrrell Museum of Palaeontology, Drumheller, Alberta, kindly identified the *Gryphaea* shells. Dr. Paul J. Young, Department of Zoology, University of Alberta, supplied the equipment for smoking the burrow. The Montana Department of Fish, Wildlife and Parks and the Alberta Department of Culture and Multiculturalism (Provincial Museum) provided partial funding for the project and allowed Flath, and Burns and Milot, respectively, to participate. Archaeological clearance for excavation was obtained from John Taylor, BLM archaeologist, Billings, Montana, Resource Area. Hugh C. Smith, Provincial Museum of Alberta, and two anonymous referees reviewed the paper and thus improved it. This is Provincial Museum of Alberta Natural History Contribution No. 101.

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BIBLIOGRAPHY AND SUBJECT INDEX OF THE PRAIRIE SKINK, *EUMECES SEPTENTRIONALIS* (BAIRD) (SAURIA: SCINCIDAE)

Louis A. Somma[1] and Philip A. Cochran[2]

ABSTRACT.—The prairie skink, *Eumeces septentrionalis*, is a small, semifossorial lizard inhabiting the tall-grass prairies and savannas of the central lowland province region of North America. This study provides an extensive bibliography and subject index as a tool for current and future workers studying *E. septentrionalis* and related species.

The prairie skink, *Eumeces septentrionalis*, is a small, semifossorial lizard (family Scincidae) inhabiting tall-grass prairies and savannas of the central lowland region of North America (Breckenridge 1941a, 1943b, Taylor 1935, Smith and Slater 1949, Nelson 1963). Although *E. septentrionalis* was not formally described until 1858 (Baird), an obvious informal description was made by Schoolcraft (1834, discussed by Breckenridge 1941a, 1943b, 1981, Somma 1985a).

The two subspecies of *E. septentrionalis* currently recognized include the northern prairie skink, *E. s. septentrionalis* (Baird 1858, see also Baird 1859, Taylor 1935), and the southern prairie skink, *E. s. obtusirostris* (Bocourt 1879, see Taylor 1935). Smith and Slater (1949) described *E. s. pallidus* from Texas, a subspecies not currently recognized (Collins et al. 1982, Dixon 1987). While possible intergrades between *E. s. septentrionalis* and *E. s. obtusirostris* may exist in northern Oklahoma (Webb 1970) and Woodson County, Kansas (Clarke 1956), these specimens may require further study as it has been suggested that populations of these two subspecies in Kansas are isolated (Collins 1982).

Eumeces septentrionalis has received some attention in studies concerning its natural history (Breckenridge 1941a, 1943b, Nelson 1963, Bredin 1981, 1989 [personal communication]), physiological ecology of its eggs (Somma 1989c, unpublished data), and most recently its brooding behavior and nesting ecology (Somma 1985a, 1985c, 1987a–c, 1989a, 1989b, McAllister 1987, Somma and Fawcett 1989). Most of these studies have dealt with the northern subspecies, as little knowledge of the biology of *E. s. obtusirostris* is currently available.

Several authors have provided bibliographies of the prairie skink in their respective studies (Breckenridge 1941a, Nelson 1963, Somma 1985a, Cochran and Somma, in press). These literature reviews are somewhat abbreviated or lacking in completeness. The objectives of this survey are to provide an extensive bibliography and subject index to *E. septentrionalis* as a resource for current and future workers in saurian biology, particularly in the prairie states, and to stimulate further interest in studying the biology of *E. septentrionalis*. We would appreciate being informed of any errors or omissions in our survey.

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TAXONOMY AND SYSTEMATICS.—Baird 1858, 1859, Cope 1875, 1880, 1900, Bocourt 1879, 1881, Ortenburger 1927, Taylor 1935, Breckenridge 1941a, 1943b, Smith and Slater 1949, Smith and Smith 1952, Clarke 1956, Cochran 1961, Nelson 1963, Smith et al. 1964, McCoy and Richmond 1966, Somma 1985a, Cochran and Somma, in press.

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DISTRIBUTION, STATES (INCLUDING MEXICO).—Note: Seehorn's (1982) records for *E. s. obtusirostris* in Florida, Arkansas (Ozark National Forest only), Mississippi, Louisiana, and Tennessee are highly erroneous and probably represent misidentified *E. anthracinus*. We recommend that this publication not be used as a reference to the status and distribution of *E. septentrionalis*.

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ACKNOWLEDGMENTS

We owe a debt of gratitude to J. Mundell, L. Valentine, and the late M. Covault (Interlibrary Loan Department, University Library, University of Nebraska at Omaha) for the superb library skills they used in helping us obtain literature. We are sincerely thankful to James D. Fawcett for his help, encouragement, and use of his extensive herpetological library.

We thank J. W. Lang, H. A. Dundee, S. E. Trauth, J. T. Collins, H. M. Smith, and J. D. Lynch for providing us with crucial references. We are indebted to E. J. Bredin for giving us permission to cite his unpublished manuscript.

P. A. Cochran was supported by a summer grant from the St. Norbert College Faculty Development Program.

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ORIENTATION OF ZOOPLANKTON TO THE OXYCLINE IN BIG SODA LAKE, NEVADA

Michael A. Bozek[1]

Abstract.—Zooplankton in meromictic Big Soda Lake, Nevada, were sampled in October 1982 to determine species composition and vertical distribution relative to the oxycline. *Moina hutchinsoni* was most abundant in the epilimnion, but prior to migrating into the anoxic hypolimnion, it aggregated at the oxycline. *Brachionus plicatilis* was most abundant below the oxycline. Concentrations of *Brachionus* and *Moina* near the oxycline corresponded with peaks in bacterial productivity found by previous investigators. However, further investigation should be conducted to verify feeding by zooplankton primarily in the anoxic hypolimnion.

Big Soda Lake is an ectogenic meromictic crater lake located near Fallon, Nevada (39°31′N, 118°52′W). A remnant of pluvial Lake Lahontan, Big Soda Lake has undergone considerable change because irrigation of the surrounding area has increased the water table and lake level, thus resulting in reduced salinity and increased chemocline depth (Hutchinson 1957, Kimmel et al. 1978).

Hutchinson (1957) predicted that meromictic conditions in Big Soda Lake might persist for several centuries, but Kimmel et al. (1978) predicted the meromixis would continue for only several decades. Changes in the physical-chemical properties of the saline lake environment are likely to modify the structure of the biotic community that is presently adapted to Big Soda Lake. The purpose of this study was to determine the vertical distribution of the major zooplankton taxa relative to the present location of the oxycline in Big Soda Lake.

Methods

The vertical distribution of zooplankton was sampled in Big Soda Lake, Nevada, on 30–31 October 1982. Zooplankton were sampled at 2-m intervals, from the surface to a depth of 20 m, with additional samples collected at 25, 30, and 35 m. Sampling was conducted every four hours at 1230, 1630, 2030, 0030, and 0830 during a single 24-hr period. No sample was collected at 0430. Oxygen, temperature, and conductivity profiles of the lake were measured using a portable Hydrolab water analyzer unit (Hydrolab Corporation, Austin, Texas).

A 6-l Van Dorn bottle was used to collect zooplankton. Each sample was filtered through 63-um mesh Nitex netting and preserved immediately in 10% formalin + 60 g/l sucrose. All zooplankton were counted and identified to species. Specimens of the cladoceran *Moina hutchinsoni* were also differentiated by sex. Results are presented for each species as the percent of the population occurring at each depth during each sampling period.

Results

Big Soda Lake was stratified during sampling, with the thermocline and oxycline located at 16 cm (Fig. 1). Changes in conductivity indicated that the chemocline was located at 32 m.

Eight species of zooplankton were found in Big Soda Lake. *Moina hutchinsoni* was the most abundant species, comprising over 90% of the individuals collected. An average of 8.8 males and 13.4 females per liter were present in all samples combined. Rotifers *Brachionus plicatilis* and *Hexarthra mira* averaged 1.1 and 0.9 individuals per liter, respectively. Less abundant species included *Bosmina longirostris*, *Diaptomus sicilis*, *Lecane lunaris*, *Dropterus* sp., and *Polyarthra vulgaris*.

Moina hutchinsoni was located primarily in the epilimnion during this survey (Fig. 2). Both males and females appeared to make vertical migrations during the 24-hr sampling period, but migrations appeared to be

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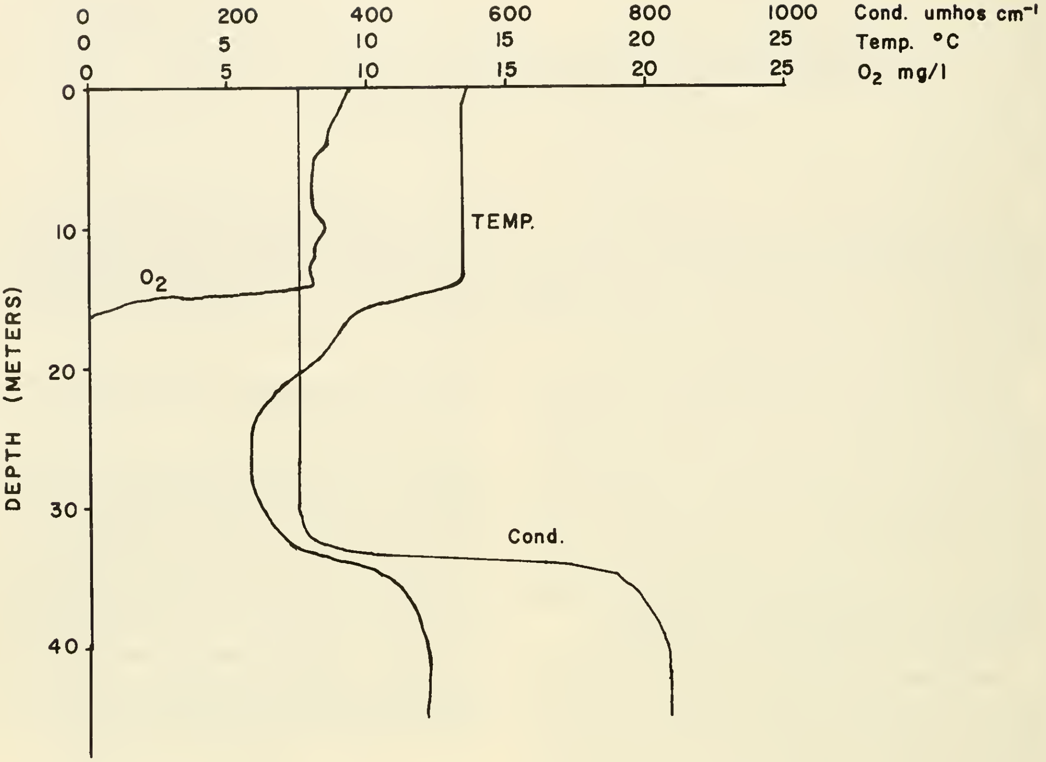

Fig. 1. Vertical profiles of conductivity, temperature, and oxygen in Big Soda Lake, Nevada, 31 October 1982.

different. Males consistently attained a greater mean depth than females, and proportionally more males entered the anoxic hypolimnion. Aggregations by both sexes were associated with the 16-m oxycline depth, but aggregating was more pronounced in males. During the greatest descent of the vertical migration, nearly 25% of the males were located within the anoxic hypolimnion.

The distribution of *Brachionus plicatilis* occurred primarily in the anoxic hypolimnion throughout most of the sample period (Fig. 3). Plating in *Brachionus* occurred at 20 m rather than at the 16-m oxycline depth found in *Moina*. At least 50% and as much as 75% of the *Brachionus* was always present in the anoxic hypolimnion.

DISCUSSION

Aggregations of both *Moina* and *Brachionus* congregated at or near the oxycline during part of the sampling period. *Brachionus* was primarily located below the oxycline at 20 m. *Moina*, however, was more abundant in the epilmnion and aggregated at the oxycline prior to entering the anoxic hypolimnion during vertical descents.

Zooplankton in Big Soda Lake may be orienting to the oxycline to utilize autotrophic bacteria as a food resource. During stratification, bacterial chemosynthesis and photosynthesis in the anoxic hypolimnion contribute greater than 80% of the primary productivity to Big Soda Lake (Cloern et al. 1983b), with peak productivity several meters below the oxycline (depths of 20–25 m) (Axler 1978, Priscu et al. 1982, Cloern 1983a, 1983b). Zooplankton are known to concentrate near, and feed on, autotrophic bacteria occurring near oxyclines in lakes (Sorokin 1958, Sorokin and Donato 1975, Takahashi and Ichimura 1968). The largest concentrations of *Brachionus* in this study occurred at 20 m, which corresponds to the depth at which maximum productivity has been reported (Axler et al.

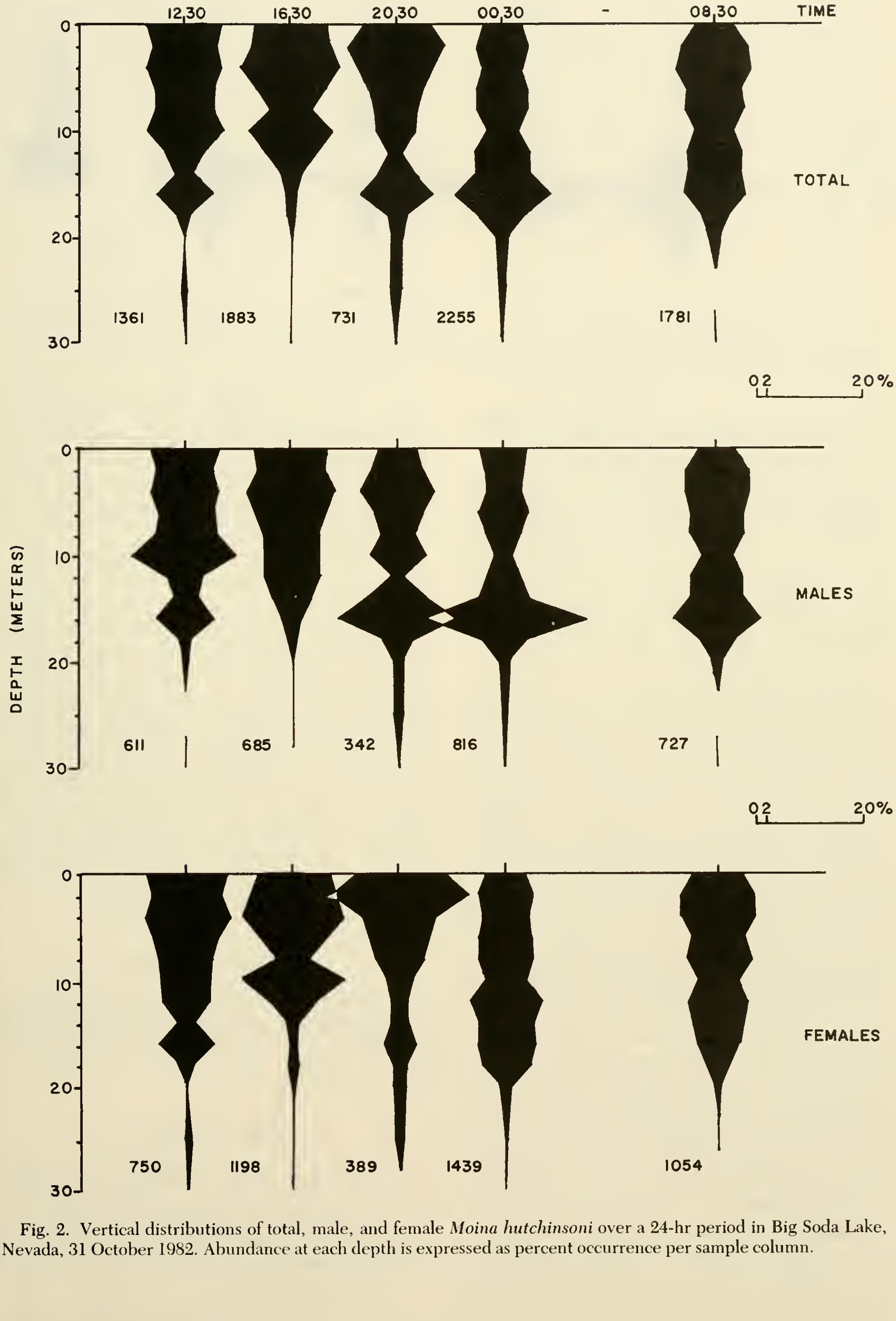

Fig. 2. Vertical distributions of total, male, and female *Moina hutchinsoni* over a 24-hr period in Big Soda Lake, Nevada, 31 October 1982. Abundance at each depth is expressed as percent occurrence per sample column.

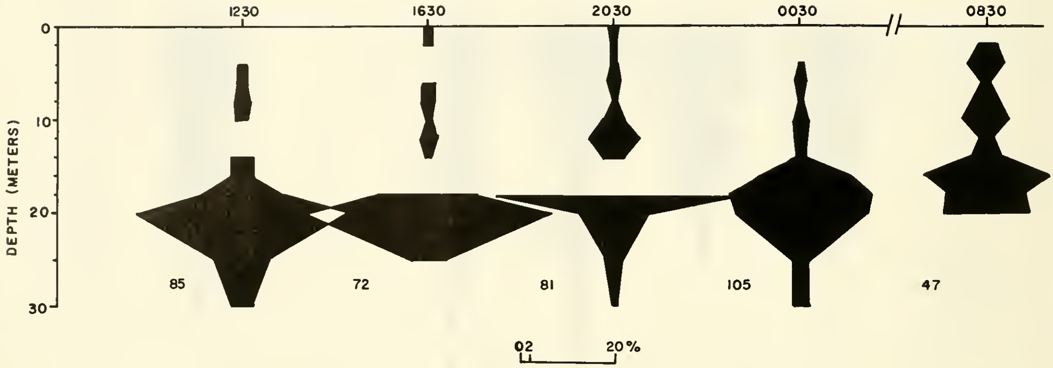

Fig. 3. Vertical distributions of *Brachionus plicatilis* over a 24-hr period in Big Soda Lake, Nevada, 31 October 1982. Abundance at each depth is expressed as percent occurrence per sample column.

1978, Cloern et al. 1983a, 1983b). No physical-chemical boundary was detected at 20 m that might otherwise explain this large aggregation of *Brachionus*. Rotifer tolerance for low oxygen levels has been described on several occasions (Larsson 1971, Ruttner-Kolisko 1975, Miracle and Vicenti 1983) and may provide a means to effectively reduce competition with *Moina* for the food resources in Big Soda Lake. At this depth *Brachionus* is deeper than 98% of the migrating *Moina*.

Vertical migration, such as occurred in *Moina*, often is associated with foraging. Physiologically, however, *Moina* may be able to access only the top portion of this productivity plate as indicated by its migration depth. Devol (1981) found that reduced oxygen prevented vertical migration of zooplankton in two British Columbia fjords. If reduced oxygen decreases the ability of *Moina* to migrate into the anoxic hypolimnion, then *Moina* present in the anoxic hypolimnion may have been only transient, and aggregations may indicate that *Moina* staged at the oxycline prior to moving into the anoxic hypolimnion.

Changes in zooplankton density occurred throughout the study period, which is not uncommon in vertical migration studies of zooplankton (Miracle 1977, Gophen 1979). Unfortunately, zooplankton migration studies rarely use replicates (Bohrer 1980, Culver and Brunskill 1969, Miracle and Vicente 1983) because the greater time required to collect extra samples increases the time zooplankton can migrate between sample depths. This then reduces the accuracy of any profile for any particular sample time. For this reason, a single, large (6-l) sample was taken at each depth. Although differences in zooplankton density occurred, the vertical distributions of *Moina* and *Brachionus* are clearly different and are related to the oxycline, suggesting that some type of resource partitioning may be occurring.

Brachionus and *Moina* in Big Soda Lake orient to the oxycline and enter the anoxic hypolimnion during at least some portion of the day. Food resources located in the anoxic hypolimnion may be one reason for this anomalous distribution and warrant further investigation. With the continual dilution of Big Soda Lake from surrounding irrigation, changes in the structure of the biotic community can be expected to occur. This study suggests that the present distributions of and resource partitioning by zooplankton may change as the physicochemical conditions governing the location of the oxycline and productivity of the lake also change.

ACKNOWLEDGMENTS

I thank Frank J. Rahel, Wayne A. Hubert, Michael Parker, and Gene R. Wilde for their helpful review comments on earlier drafts of this manuscript.

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COEXISTENCE OF TWO SPECIES OF SUCKER, *CATOSTOMUS*, IN SAGEHEN CREEK, CALIFORNIA, AND NOTES ON THEIR STATUS IN THE WESTERN LAHONTAN BASIN

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ABSTRACT.—The observed distribution and relative abundance of two morphologically similar species of sucker, *Catostomus*, have shifted dramatically over the past four decades in Sagehen Creek and nearby streams in eastern California. The mountain sucker, *C. platyrhynchus*, formerly abundant and more numerous than the Tahoe sucker, *C. tahoensis*, has become relatively rare and during this study was consistently less abundant than the Tahoe sucker at all eastern California sites in 1983. Similar shifts in abundance were not seen at the three Nevada sites. Behavioral observations and data on spatial and temporal patterns of habitat use, collected in Sagehen Creek between May and September 1982 and 1983 using a snorkel survey method, indicate nearly complete overlap between mountain and Tahoe sucker habitat use and an absence of any agonistic behavioral interaction between species. The decline of the mountain sucker in these areas is likely the result of an interaction of loss of habitat due to reservoir construction and destructive management practices. These changes may have led to the elimination of isolating mechanisms between the two species and may be increasing the opportunity for introgressive hybridization.

The mountain sucker, *Catostomus platyrhynchus*, and the Tahoe sucker, *C. tahoensis*, co-occur in Sagehen Creek and other streams in the Lahontan drainage basin of eastern California and west central Nevada (Moyle 1976). They are morphologically similar, and natural hybrids occur (Hubbs et al. 1943, Smith 1966). The more widely distributed mountain sucker has been considered a product of *Catostomus* evolution, specialized for cool waters, rapid currents, and rocky substrates (Smith 1966). The Tahoe sucker, endemic to the Lahontan Basin, is considered a stream generalist and reaches greatest size and numbers in lakes and reservoirs (Willsrud 1966, Vigg 1978, Marrin et al. 1984). Although superficially similar, the mountain sucker differs from the Tahoe sucker in morphologic trophic specializations (Smith 1966), including small terete bodies, reduction of swim bladder size, and lip and jaw modifications for scraping diatoms and algae from rocks. Moyle (1976) indicated that the two species probably segregate spatially in streams, the mountain sucker being more abundant in upper stream reaches and the Tahoe sucker more abundant in lower stream reaches; when the two species are found together, the mountain sucker is thought to concentrate in riffle sections while the Tahoe sucker inhabits pools.

In 1982, distribution, abundance, habitat use, and behavioral interactions were observed and quantified in Sagehen Creek to determine possible mechanisms allowing the continued coexistence of these two sympatric species. During this time, the mountain sucker was extremely scarce, whereas earlier surveys found the mountain sucker to be equally as abundant as or more abundant than the Tahoe sucker (Flittner 1953, Gard and Flittner 1974). Collections in nearby streams also turned up few mountain suckers. In 1983 I began an intensive survey over a full summer season to determine the distribution, abundance, habitat use, and behavioral interactions of both species in Sagehen Creek, and an extensive survey of other sites where both species had been previously located, to determine if the change in relative abundance was widespread. These results provide background data essential for evaluating the prospects for continued coexistence of these two species in light of the extensive modification of their habitats (primarily reservoir construction), which has occurred over the last four decades.

STUDY AREAS

Principal Study Stream: Sagehen Creek

Sagehen Creek is in the Tahoe National Forest, 12.1 km north of Truckee, California

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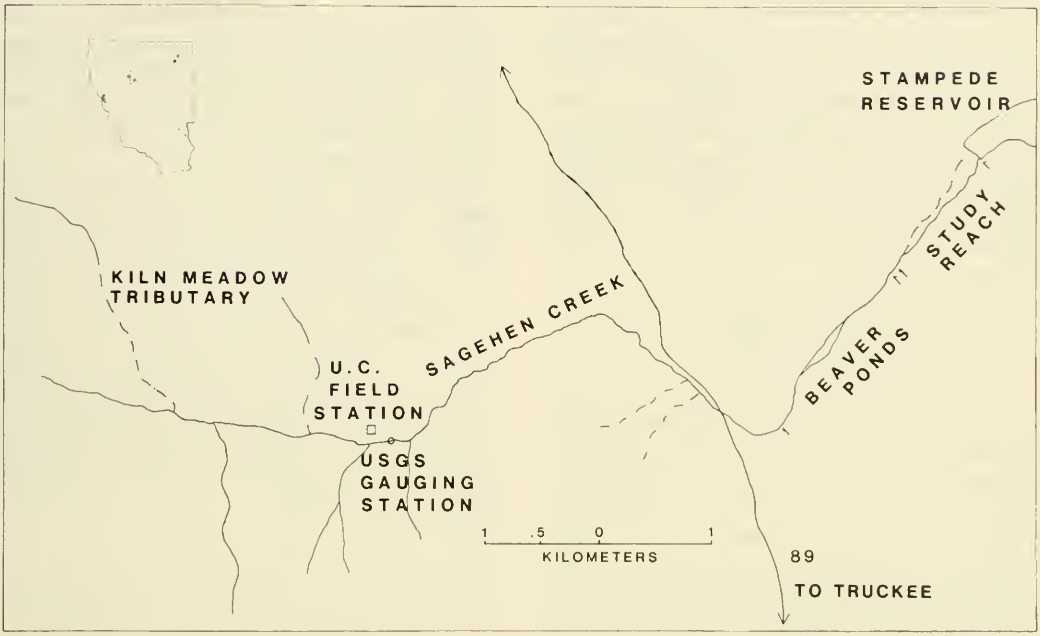

Fig. 1. Location of the principal study site at Sagehen Creek, California, and the extensive comparison sites from previous surveys (inset: □ = Sagehen Creek, Little Truckee River, Prosser Creek, Martis Creek; ○ = tributary to the Carson River; ● = Hot Creek; △ = North Fork of the Humboldt River).

(Fig. 1). It originates from a series of small springs at an elevation of 2,256 m on the east side of the Sierra Nevada. Prior to the filling of Stampede Reservoir in 1969, Sagehen Creek meandered an estimated 20.3 linear km through several small meadows, a riparian corridor of lodgepole pine (*Pinus contorta*), mountain alder (*Alnus tenuifolius*), aspen groves (*Populus tremuloides*), and finally a larger meadow area with scattered lodgepole pine and willow (*Salix* spp.), before joining the Little Truckee River at an elevation of 1,768 m. At capacity, the reservoir inundates about 4.8 linear km and, due to the braided nature of the channel, 10.6 of the original 12.0 km of stream habitat in this area.

The study reach, located in the lower meadow area, was chosen after preliminary observations in 1982 because it contained the majority of the sucker populations, its boundaries were well defined by beaver dams above and Stampede Reservoir below, and few obstacles would be encountered in obtaining data by a snorkel survey method. The reach is 1,200 m in length and is contained in Sec. 3, T18N, R16E, and Secs. 34 and 35, T19N, R16E, of the U.S. Geological Survey Map, Hobart Mills, California, NW/4 Truckee Quadrangle. The reach was marked into 12 sections, 100 m each, making location of observations more easily quantifiable. Sections were numbered beginning at the upstream end of the reach and were added as the reservoir level decreased. Elevations at the section markers were referenced to the known surface level elevation of the reservoir, and altitudinal differences along the stream gradient were determined with an Abney level.

The stream meanders through a series of runs with side pools and shallow riffles. The upper 400 m is shaded by lodgepole pine, and the lowermost 800 m is open meadow with occasional willow clumps on the bank edges. The streambed is low gradient (1%), and the substrate is mostly gravel and cobble deposited on the lacustrine sediments of former Pleistocene Lake Truckee. Stream depths in late July (mean daily discharge, 0.54 m^3/sec) ranged from 0.03 m in riffle sections to approximately 1.7 m in the deepest pool. Average depth from 25 cross sections was 0.35 m, and average width was 5 m. The water was clear and visibility was 2 m or greater on all snorkel observation days.

In addition to Tahoe and mountain suckers, seven other species of fish inhabit the study reach either as residents or migrants: mountain whitefish (*Prosopium williamsoni*), rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), Lahontan speckled dace (*Rhinichthys osculus robustus*), Lahontan redside (*Richardsonius egregius*), and Paiute sculpin (*Cottus beldingi*).

Extensive Site Comparisons from Previous Surveys

Little Truckee River, Sierra Co., California, 100 m upstream of the Highway 89 bridge crossing 18 km north of Truckee, California, in Sec. 20, T19N, R16E, U.S.G.S. Truckee, California-Nevada 15 min. Quad. 1955. Elevation 1,877 m. This site was the same as that of Hubbs et al. (1943).

Sagehen Creek, Sierra and Nevada cos., California, two sections within the 1.2-km reach above Stampede Reservoir. Secs. 34 and 35, T18N, R16E, Sec. 3, T19N, R16E, U.S.G.S. Truckee, California-Nevada 15 min. Quad. 1955. Elevation 1,815 m (est.). These are two of three sites (Stations VII and IX) used by Flittner (1953) and Gard and Flittner (1974). The third site and possibly portions of the lower section (IX) surveyed in 1983 are inundated by Stampede Reservoir.

Prosser Creek, Nevada Co., California, 50 m below the Highway 89 bridge crossing 7.2 km north of Truckee, California, Sec. 22, T18N, R16E, U.S.G.S. Truckee, California-Nevada 15 min. Quad. 1955. Elevation 1,756 m. This site is about 1.7 km upstream from the 1942 old highway bridge survey site (Hubbs et al. 1943), which was inundated when Prosser Reservoir was impounded in 1963. The difference in elevation between the 1942 and 1983 sites is about 50 m.

Martis Creek, Nevada Co., California, reach below Martis Reservoir (Moyle and Vondracek 1985). Secs. 5 and 8, T17N, R16E, U.S.G.S. Truckee, California-Nevada 15 min. Quad. 1955. Elevation 1,740 m (est.). This site is below the 1939 survey area (Alex J. Calhoun, California Academy of Sciences, San Francisco, unpublished data), which was inundated when Martis Reservoir was impounded in 1971.

Tributary to the Carson River at Dayton, Lyon Co., Nevada. The tributary enters the Carson River under Ricci Road Bridge crossing. Sec. 23, T16N, R21E, Nevada Department of Transportation map 6-12, 1980. Elevation 1,463 m (est.). This tributary flows into the Carson River at the 1942 (Hubbs et al. 1943) survey site.

Hot Creek, Eureka Co., Nevada. Sec. 9, T28N, R52E, Nevada Department of Transportation map 4-5, 1959. Elevation 1,585 m (est.). This site was the same as that of Hubbs et al. (1943).

North Fork of the Humboldt River, Elko Co., Nevada, at Interstate 80 bridge crossing between Elko and Wells, Nevada. Sec. 3, T38N, R57E, Nevada Department of Transportation map 3-4, 1976. Elevation 1,585 m (est.). This site was the same as that of Hubbs et al. (1943).

METHODS

Principal Study Stream: Sagehen Creek

Distribution and abundance.—Surveys to estimate the total distribution and abundance of suckers within the entire 1,200 m Sagehen Creek study reach were completed once every two weeks from 7 June to 30 August 1983 and again on 22 September 1983. Number, age class (juvenile or adult), and location of each surveyed individual were recorded. Additional observations were made of the composition of fish assemblages when fish appeared in groups and of characteristics of the habitat.

High water on 7 June and 22 June made visibility poor. Surveys were therefore completed by electrofishing from the bottom to the top of the study reach using a Smith-Root Type V backpack electrofisher. Remaining surveys were completed by snorkel survey (Goldstein 1978).

Observations were made while I pulled slowly upstream along the bottom in a shallow switchback pattern looking for fish at the banks, near or under obstructions, among rocks, in riffles, and in the mainstream. By this method, I observed fish upstream without having an obvious effect on their behavior.

Environmental factors.—A U.S. Geological Survey stream gauging station, 7.9 km below the headwaters of Sagehen Creek, measures the discharge from a drainage area of 27.2 km^2 (Fig. 1). Continuous stage and discharge records have been collected since

December 1953. Stream temperature is recorded at the Sagehen Creek Field Station by a Taylor continuous recording air and water thermograph, calibrated monthly. Stream temperatures also were taken in the study reach with a Taylor pocket thermometer for comparison with temperatures at the field station. Reservoir level elevation was provided by the U.S. Bureau of Reclamation. A water-stage recorder with a mercury-column manometer located at Stampede Dam has been in operation since August 1969.

MICROHABITAT USE.—Microhabitat use of the two sucker species was quantified in Sagehen Creek in both 1982 and 1983. Fish were located using the snorkel survey method described. The following data were recorded for each fish observed: stream section (riffle, pool, pool-run edge, or run), general location of fish and description of site, water temperature, water velocity taken at fish snout (focal point velocity), water velocity taken at 0.6 total depth (mean water column velocity), depth of water column at fish (maximum depth), distance from the water surface to the fish (focal point depth), substrate composition in a 0.25 m^2 area beneath the fish, amount and type of aquatic vegetation including an estimate of filamentous algae cover on the stream bottom, amount of shade, and description and proximity of the closest cover.

Water current velocities were measured to the nearest 0.3 cm sec^{-1} with a Gurley Pygmy Current Meter mounted on a top-setting wading rod. Depths were measured to the nearest 3 cm directly from the rod. I estimated visually the substrate size composition based on a modified Wentworth particle size scale (Bovee and Milhous 1978).

Because of time constraints and the scarcity of fishes in the reach during many sample periods, I used an opportunistic (thus nonrandom) sampling scheme to collect microhabitat measurements. Measurements were taken systematically, working from the bottom to the top of the reach between the hours of 1100 and 1500 and quantifying microhabitats as fish were encountered. These measurements were taken independently of distribution and abundance surveys. The Spearman's rank correlation is used as a descriptive tool to display and compare similarity of the ranked frequency distributions of various microhabitat factors between the two species for each observation.

BEHAVIORAL OBSERVATIONS.—Throughout the study, I observed at each site the species, number, and size of associated fish, and any interaction among fishes. In 1982 I observed fish by snorkeling at sites in the study reach for two to five 30-minute intervals on seven different occasions. In 1983 fish were observed for 30- to 45-minute intervals in the study reach on three separate occasions. In addition, over the two-year study period, 434 separate observations of behavior were collected in association with the microhabitat-use measurements.

For comparison, the diel behavior and activity patterns of both species of sucker were quantified in an underwater stream observation tank at the Sagehen Creek Field Station, where flows and water depth are regulated at the top and bottom of a diversion channel. The observation area was 9.1 × 2.6 m, with a grillwork at each end to keep the fish inside. Dividers were also used to confine fish in three enclosures, each roughly 3.0 × 1.2 m, next to the glass. Artificial cover was provided by floating a small piece of plywood in each enclosure.

Fish were captured by electrofishing in Sagehen Creek and nearby Little Truckee River, and were then transported to the field station in chests containing cooled stream water. Fish were weighed, measured, and placed in the enclosures for a two-day acclimatization prior to the observations. Three sets of observations were made of the behavior and activity of the two species between 21 July and 6 September 1982. The first two sets were composed of twelve 4-hr periods (twice covering the full 24 hrs), conducted over two 2-week periods. The final set was composed of twelve 2-hr periods (once covering a full 24 hrs) of observation over one week. In the first two sets I recorded behavior and activity of Tahoe suckers at three densities: 1, 5, and 6 fish per enclosure (0.3, 1.4, and 1.7 per m^2). In the final set I recorded the interaction of Tahoe and mountain suckers in two mixtures: 2 Tahoe and 4 mountain suckers, 5 Tahoe suckers with 1 mountain sucker, and, for comparison, 6 Tahoe suckers alone. These densities were similar to observed densities in lower Sagehen Creek for similar areas where suckers commonly occurred in groups ranging

TABLE 1. Temporal distribution, abundance, and group size of suckers within the Sagehen Creek study reach from 7 June to 22 September 1983 (* indicates that fishes were present only in a diversion of the main stream).

	Fish distribution			Sucker abundance			Group size		
Survey date	Total distribution (meters)	Distribution through sections	Total sites where present	Tahoe juveniles	Tahoe adults	Mountain adults	$\bar{x}$	S.D.	Range
6/7	1*	7	2	0	5	0	2.5	2.1	1–4
6/21	570	6–12	9	0	73	0	8.1	12.5	1–40
7/5	630	6–12	18	0	75	0	4.2	4.5	1–16
7/19	588	4–10	14	0	77	1	5.6	6.7	1–25
8/2	855	2–11	32	51	154	37	7.6	8.3	1–30
8/16	840	4–12	26	75	83	34	7.4	7.1	1–28
8/30	630	4–10	16	44	31	5	5.0	4.6	1–17
9/22	392	7–11	4	8	1	0	2.3	1.5	1–4

from 1 to 40 ($\bar{x} = 5.3$, Table 1). During all sets, the type and number of activities (feeding, swimming, resting on the stream bottom) per fish per minute in each enclosure were recorded (10 minutes at each enclosure, and two 10-minute periods per enclosure per hour). The results are based on a total of 71.3 hours of observation.

EXTENSIVE SITE COMPARISONS FROM PREVIOUS SURVEYS

I examined the relative abundance of suckers at seven Lahontan Basin sites between July and August 1983 where previous data were available (Hubbs et al. 1943, Flittner 1953, Erman 1973, Gard and Flittner 1974) (Alex J. Calhoun, California Academy of Sciences, San Francisco, unpublished data; Don C. Erman, University of California, Berkeley, unpublished data; Joseph J. Cech, and Peter B. Moyle, University of California, Davis, unpublished data). Seven stream segments that could be precisely relocated from original field descriptions were resurveyed. Six sites were sampled with Smith-Root backpack electrofishers. The North Fork of the Humboldt River site was sampled with a 457 × 183 × 0.64-cm mesh seine.

Stream temperature, sample section length, average width and depth, characteristics of the stream bottom, aquatic vegetation present, and water clarity were noted. A general description of the area and the degree and type of human or animal disturbance evident at each site was also documented. Fishes were identified, counted, and usually released at the sites. Specimens collected for further analysis or for use as museum specimens (deposited at California Academy of Sciences, San Francisco) were preserved immediately in 10% buffered formalin and later transferred to 70% ethanol solution for storage.

Sampling was systematic and based on current knowledge of technique, stream conditions, and behavior of the target populations. These criteria are considered to have been met by the earlier surveys used for comparison. In a purely statistical sense, between-year samples employing different techniques are noncomparable; however, I felt the systematic method of sampling (past and present) should produce representative estimates of the Tahoe-to-mountain sucker ratios at each site and would allow use of the chi-square test for descriptive purposes. Previously, Dauble and Gray (1981) compared use of a small seine and backpack electroshocker, finding similar catch frequencies for catostomids with both types of gear.

RESULTS

Sagehen Creek

DISTRIBUTION AND ABUNDANCE.—Tahoe suckers were distributed throughout the Sagehen Creek study reach and occurred in both 1982 and 1983 as far upstream as 400 m above the Highway 89 bridge crossing. In 1982 one Tahoe sucker was caught entering the Kiln Meadow tributary 5.6 km above the highway bridge (Fig. 1). The distribution of mountain suckers was limited to the lower 1,100 m of the study reach in both years.

In the initial survey, during a period of high discharge on 7 June 1983, 5 adult Tahoe suckers were present at one site about 260 m above the reservoir (Fig. 2). Between the 7 June and

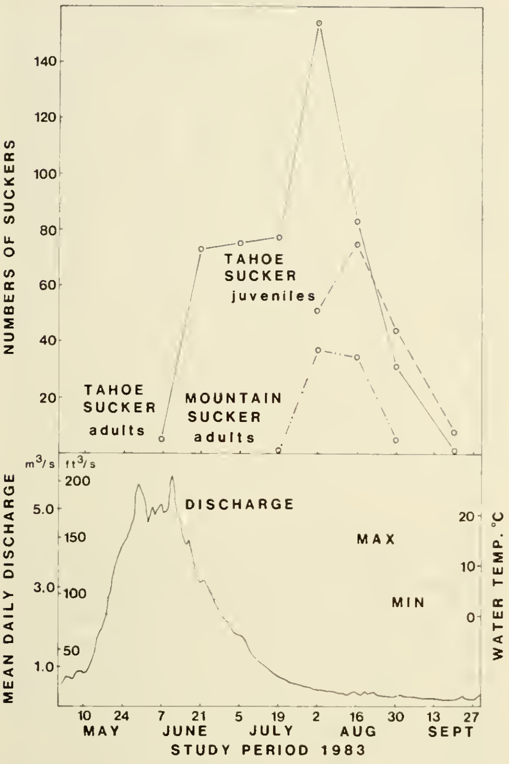

Fig. 2. Temporal abundance of suckers in the study reach with corresponding measurements of mean daily discharge and maximum and minimum daily stream temperatures at University of California's Sagehen Creek Field Station.

21 June surveys, mean daily discharge decreased and stream temperatures increased. Correspondingly, the number of Tahoe sucker adults observed increased to 73. On 22 June, Tahoe suckers were observed spawning in an open gravel riffle at the 790-m mark.

Mountain suckers were first observed in the reach on 19 July, when one individual was found. By the following survey of 2 August, the observed number of mountain suckers increased to 37, and Tahoe sucker juveniles also appeared in the reach (Fig. 2). Tahoe sucker juveniles occurred in groups with, and were always more abundant than, the similarly sized mountain sucker adults. Observed numbers of mountain sucker (37) and Tahoe sucker adults (154) peaked on 2 August. Numbers of juvenile Tahoe suckers peaked (75 individuals) in abundance on 16 August. As individuals counted began to decline, stream temperature was also declining (Fig. 2). Mountain suckers were not seen in the reach after the 30 August survey. I assumed that they had spawned, as breeding tubercles were present on most individuals, but spawning was not observed. Young-of-the-year suckers of either species were not observed in 1983. By the final survey of 22 September, very few Tahoe sucker individuals remained; only 1 adult and 8 juveniles were found in the reach.

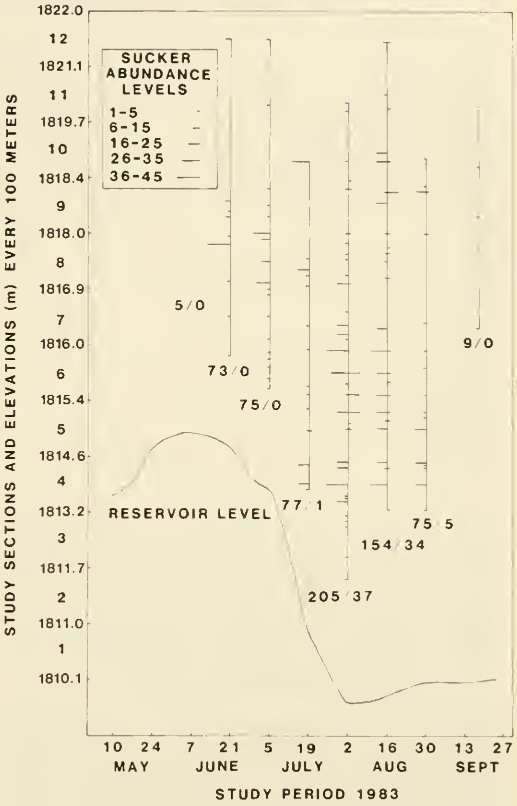

Fig. 3. Temporal changes in distribution of suckers and corresponding changes in reservoir level (survey starting point). Sucker abundance is shown by horizontal lines (Tahoe suckers to the left, mountain suckers to the right). Total abundance (Tahoe suckers/mountain suckers) is shown below each vertical line. Indicated elevations are at section boundaries.

Between 7 June and 21 June, when the first large group of Tahoe suckers migrated into the reach, they were distributed from Sec. 6, 160 m above the existing influence of the reservoir, through Sec. 12, 730 m above the reservoir (Fig. 3). The total longitudinal distribution of suckers observed in the study reach increased with increasing fish abundance and receding reservoir level (Fig. 3).

TABLE 2. Tahoe and mountain sucker microhabitat use measurements in Sagehen Creek, 1982–1983 summary.

	Tahoe sucker				Mountain sucker			
Measurement	$\bar{x}$	S.D.	N	Range	$\bar{x}$	S.D.	N	Range
Focal point velocity (m/sec)	0.20	0.15	385	0–0.81	0.20	0.09	39	0–0.35
Focal point depth (m)	0.56	0.20	385	0.13–0.95	0.61	0.09	39	0.47–1.82
Mean water column velocity (m/sec)	0.30	0.24	385	0–1.04	0.34	0.15	39	0.11–0.51
Water column depth (m)	0.56	0.20	385	0–0.82	0.61	0.09	39	0.47–1.01
Substrate size category	5.2		385	1–8	6.1		39	5–8
Shade (%)	49	42.6	385	0–100	45	41.8	39	0–100
Algae cover (%)	38	49.0	385	0–100	75	12.6	39	45–95
Stream section occurrence (frequency)								
Pool	0.41		156		0.33		13	
Pool-run	0.20		78		0.49		19	
Run	0.39		151		0.18		7	
Riffle	0		0		0		0	
Total fish represented			385				39	
Juveniles			53				0	
Adults			332				39	

Peak storage in the reservoir occurred on 7 June when an area encompassing 540 m of the stream reach was inundated (Fig. 3). Water was gradually released from the reservoir, and by the 2 August survey date 12 sections of the study reach were exposed stream. As water was released and lower stream sections were exposed, the distribution of suckers expanded downstream. Observed maximum upstream distribution was attained by the 21 June survey for Tahoe suckers but not until the 16 August survey for mountain suckers.

As the number of suckers increased in the reach, the pattern of the distribution sample changed from 5 suckers present at one location on 7 June to 242 suckers distributed along 855 m of the reach and 32 different sites on 2 August (Table 1). Although lone suckers were sometimes present at a site, they usually occurred in groups around cover. The observed mean group size increased as the total number and total distribution of suckers increased, with the exception of the 21 June sample (Table 1). Group size decreased as suckers began leaving the stream in late August. Rarely were solitary individuals of either species found in the stream. Only 4% of Tahoe suckers (673 observations) and 5% of mountain suckers (88 observations) occurred in the absence of other individuals of either species. In addition, mountain suckers occurred in mixed-species groups with Tahoe suckers at 93% of the mountain sucker sites ($n = 88$ observations) between 19 July and 30 August.

MICROHABITAT USE.—The most important microhabitat factor for the Tahoe and the mountain sucker appeared to be the presence of cover. Of the 434 microhabitat measurements of sites with fish, 70.8% were recorded in, among, or very near exposed willow or tree root masses in the stream; 9.5% near undercut banks; 9.0% near log jams; and 2.5% among large boulders. Only 8.2% of the sites with fish lacked cover.

In other respects, suckers used a fairly broad range of overlapping microhabitats, with substantial variability around the means for all microhabitat variables (Table 2). Even less affinity was apparent for particular values of focal point velocity, mean water column velocity, and depth when measurements attributable to cover (willow or tree root masses) were accounted for in each distribution. Microhabitat use by mountain suckers appeared less variable than that by Tahoe suckers, but these results may reflect the small sample size (39) for mountain suckers: 8 in 1982 and 31 in 1983. Tahoe suckers seem to utilize a smaller substrate size than mountain suckers (Table 2). Mean substrate size was in the gravel category for the Tahoe sucker and in the rubble/cobble category for the mountain sucker, although the ranked frequencies were similar (Spearman's rank, $r_s = .750$; $p < .05$ [Steel & Torrie 1960]). Comparison of the distributions of ranked frequencies of the microhabitat use measurements for mean water column velocity ($r_s = .604$; $p < .05$) and focal point velocity ($r_s = .809$; $p < .001$) also showed correlation between Tahoe and mountain sucker use, indicating the species appeared to use similar proportions of the range of each habitat factor. As neither species occurred off the stream bottom, no appreciable correlation occurred between depth-use distributions ($r_s = .427$; $p < .05$).

In both 1982 and 1983, algae on the substrate became evident during the second week of July. Prior to this time only Tahoe suckers were present in the stream, and no algal cover beneath fish was observed. Comparison of estimated algae cover after the second week of July showed no difference ($p > .05$) between mountain sucker and Tahoe sucker sites in 1982 but some difference between sites in 1983. In 1982, mean algae cover for mountain sucker sites was 81% (S.D. = 11; n = 8) and for Tahoe suckers, 61% (S.D. = 41; n = 85). In 1983, mean algae cover was 73% (S.D. = 14; n = 31) and 49% (S.D. = 35; n = 181) for mountain suckers and Tahoe suckers, respectively.

Both species were distributed in pool, pool-run edge, or run habitats; no suckers were found in riffle sections (Table 2). Of habitats where Tahoe suckers occurred, 41% were in pool habitats, 39% in runs, and 20% in pool-run edges (Table 2). Mountain suckers most often occurred in pool-run edges (49%), with 33% in pool and 18% in run habitats (Table 2).

BEHAVIOR.—Both Tahoe and mountain suckers rested on the bottom of the study reach near some type of cover during the majority of daylight hours. Feeding was seldom observed until early July, and then only in the afternoon. The arrival of mountain suckers in the reach was coincident with increased algal abundance on the substrate, and mountain suckers were observed feeding substantially more often than Tahoe suckers. Mountain suckers and juvenile Tahoe suckers almost always were observed together in the reach, where they rested side-by-side on the stream bottom. Agonistic encounters were never observed during this study.

Results from the stream observation tank reinforced results of daylight observations made in the study reach. Both species were highly gregarious. They rested side-by-side, often touching under the provided cover. This behavior occurred in both mixed- and single-species groups. When movement occurred, the group acted as a unit, regardless of its make-up. Activity patterns fluctuated at low levels from early afternoon until early morning, with a 6-hour period of less activity beginning just after dawn (Fig. 4). Both species appeared more active at night. Feeding intensity was greatest during this time, and the fish moved in less tightly structured groups. Feeding-related activity accounted for a majority of the 81.3 hours of activity observed: 74.6% for solitary suckers, 54.2% for the 5-sucker group, and 62.5% for the 6-sucker group.

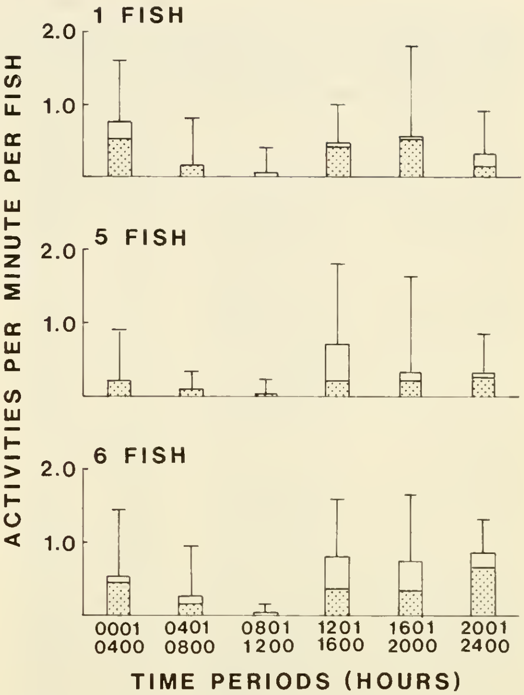

Fig. 4. Activity patterns of Tahoe and mountain suckers at three density levels in the stream observation tank (bars = the mean total activities per minute per fish; shaded portions = feeding activity per minute per fish; vertical lines = the highest value for each time period). Each 4-hour period represents 18 observation times. The results are based on 71.3 hours of observation.

Extensive Collections and Historical Comparisons

The Little Truckee River, Sagehen Creek, Prosser Creek, and Martis Creek differed significantly (chi square $p < .05$ [Steel and Torrie 1960]) in relative abundance of Tahoe and mountain suckers from early surveys (Table 3). Tahoe suckers were previously estimated to be more abundant than mountain suckers only at the Little Truckee River site (47% Tahoe, 44% mountain, and 9% hybrids in 1942 [Hubbs et al. 1943]); but in 1983, Tahoe

TABLE 3. Long-term changes in relative abundance of Tahoe and mountain suckers at seven Lahontan Basin locations. Sources are HHJ: Hubbs et al. (1943); LMD: Lynn M. Decker, unpublished field notes; GAF: Flittner (1953); DCE: Don C. Erman, University of California, Berkeley, unpublished data; PBM: Peter B. Moyle, University of California, Davis, unpublished data; AJC: Alex J. Calhoun, field collection provided by California Academy of Sciences, San Francisco. Collection methods are S = seine, E = electrofisher, P&D = pump and drain.

		Tahoe sucker		Mountain sucker		Hybrids		Collection	
Site	Date	%	No.	%	No.	%	No.	Source	Method
Little Truckee River	VIII-15-1942	47	33	44	31	9	6	HHJ	S
	VI-22-1982	80	4	20	1			LMD	E
	VII-20-1983	100	5	0	0			LMD	E
Sagehen Creek	VIII-17-1951	44	38	48	41	8	7	GAF	P&D
	VIII-27-1952	28	18	52	33	20	13	GAF	P&D
	VII-21-1971	5	3	95	57			DCE	E
	VI-22-1977	94	141	6	9			PBM	E
	VI-22-1978	96	22	4	1			JJC	E
	VIII-28-1982	57	4	43	3			DCE	E
	VIII-24-1983	87.5	7	12.5	1			DCE	E
Prosser Creek	VIII-15-1942	16	10	80	49	3	2	HHJ	S
	VII-24-1982	98	45	2	1			LMD	E
	VI-20-1983	100	9	0	0			LMD	E
	VII-8-1983	100	20	0	0			LMD	E
	VIII-5-1983	100	6	0	0			LMD	S
Martis Creek	VIII-18-1939	0	0	97	30	3	1	AJC	S
	VIII-15-1979	99	140	1	1			PBM	E
	VIII-10-1980	94	188	6	11			PBM	E
	VIII-9-1981	99	1163	1	70			PBM	E
	VIII-16-1982	95	199	5	10			PBM	E
	VIII-14-1983	95	20	5	1			PBM	E
Tributary to Carson River	VIII-20-1942	50	58	49	57	1	2	HHJ	S
	VIII-11-1983	45	4	45	4	10	1	LMD	E
Hot Creek	VIII-12-1938	9	7	87	70	4	3	HHJ	S
	VIII-12-1983	15	12	82	64	3	2	LMD	E
North Fork of Humboldt River	VII-22-1942	20	12	78	46	2	1	HHJ	S
	VIII-13-1983	29	25	70	61	1	1	LMD	S

suckers were relatively more abundant at all four California sites. In 1983 collections, Tahoe suckers comprised 100% of the suckers in the Little Truckee River, 87.5% in Sagehen Creek, 100% in Prosser Creek, and 95% in Martis Creek. This result was a reversal of the relative abundance in early surveys when mountain suckers were 48–52% of the sucker population in Sagehen Creek (Flittner 1953), 80% in Prosser Creek (Hubbs et al. 1943), and 97% in Martis Creek (Alex J. Calhoun, California Academy of Sciences, San Francisco, unpublished data).

In the tributary to the Carson River, Hot Creek, and North Fork of the Humboldt River in Nevada, the relative abundance of mountain and Tahoe suckers was not significantly different ($p > .05$) from early surveys (Table 3). In the tributary to the Carson River, equal proportions of mountain and Tahoe suckers were observed in 1942 (49% mountain, 50% Tahoe, and 1% hybrids) as compared to 1983 (45% mountain, 45% Tahoe, and 10% hybrids). In Hot Creek and the North Fork of the Humboldt River, the mountain sucker remained relatively more abundant. In Hot Creek it represented 87% of the sucker sample in 1938 and 82% in 1983; and in the North Fork of the Humboldt River, the mountain sucker represented 78% of the sucker population in 1942 and 70% in 1983.

Of the sites visited, only the Hot Creek, Nevada, site appeared unchanged from earlier descriptions. Evidence of recent human or livestock disturbance was present at all other sites. The site on the North Fork of the Humboldt River had extensive bank slumping, probably caused by cattle and horses, but it is not known if subsidence was evident in 1942. The tributary to the Carson River is controlled by a diversion structure upstream and during most irrigation seasons may remain dry continuously for several weeks (Jim Curran, Nevada Dept. of Wildlife, Fallon, personal communication).

The California streams surveyed had one change in common—reservoirs had been constructed. Sagehen Creek and Little Truckee River now flow into Stampede Reservoir (filled in 1969), Prosser Creek flows into Prosser Reservoir (filled in 1963), and Martis Creek has been bisected by Martis Reservoir (filled in 1971). Martis Creek and the Prosser Creek system were also subject to California Department of Fish and Game stream poisoning operations. Martis Creek was poisoned last in 1977 (Peter B. Moyle, University of California, Davis, personal communication), and Prosser Creek was poisoned last in 1984 (Lynn M. Decker, personal observation). Sagehen Creek has undergone little physical change upstream from the reservoir (Erman 1973), while some channelization and bank restructuring took place in 1982 at the Little Truckee site. Livestock grazing has been common at all sites.

DISCUSSION

Marked changes in the observed distribution and abundance of suckers in Sagehen Creek have occurred since Stampede Reservoir was filled in 1969 (Erman 1973). By 1975 some Tahoe sucker individuals had colonized upstream areas far above their original range. The species is now apparently a permanent inhabitant of areas above the range determined from 1952 to 1969 (Gard and Flittner 1974) and above the range of the mountain sucker. In contrast, mountain suckers occur no further upstream than they did in 1951 (Flittner 1953) and are consequently now confined to only 12% of their historical longitudinal distribution in Sagehen Creek.

Gard and Flittner (1974) speculated that the upstream limits of both species were influenced by gradient and substrate, but recent upstream movements of Tahoe suckers tend to discount this hypothesis. If the Tahoe sucker is not limited by these factors, then it is unlikely that the mountain sucker would be so limited. It is possible but unlikely that the long complex (approximately 2 km) of beaver dams and ponds above the study reach deters upstream migration of the mountain sucker but not the Tahoe sucker. Unlike Tahoe suckers, which survive very well in lakes and reservoirs (Willsrud 1966, Vigg 1978, Marrin et al. 1984), mountain suckers are thought to prefer moving water and have rarely been reported from lacustrine environments even when they inhabit tributary systems (Snyder 1983). However, my results in Sagehen Creek showed that mountain suckers leave the stream and presumably enter the reservoir in late summer, as do Tahoe suckers. Upstream migration in early summer is probably coincident with spawning, and the few adults apparently found sufficient spawning habitat below the pond sequence.

Expanded upstream movement of the Tahoe sucker may result from interaction between density-dependent factors and the availability of suitable stream habitat. It appeared that as seasonal abundance of Tahoe suckers increased in the reach, their upstream distribution also increased. Tahoe sucker abundance (Erman 1973; Don C. Erman, University of California, Berkeley, unpublished data) and size (Marrin et al. 1984) increased after filling of the reservoir. Density-dependent intraspecific interactions when population levels were high may have caused the Tahoe sucker to expand its distribution upstream where it remained once suitable habitat areas were reached (Don C. Erman, University of California, Berkeley, personal communication). Mountain suckers have decreased in abundance and now remain only in the remnants of their former habitat.

Flittner (1953) estimated the population of suckers in Sagehen Creek (1951–52) at 3,308 individuals, 49% of which were mountain suckers, 38% Tahoe suckers, and 13% considered hybrids. In 1983 the estimated maximum population in the sampled reach of Sagehen Creek was 280 suckers; 40 (14%) mountain suckers (adults) and 240 (86%) Tahoe suckers (155 adults and 75 juveniles). Because suckers migrated in and out of the stream, the relative abundance of sucker species changed over time during the study period. Thus, an overall decline in suckers in Sagehen Creek seems to have occurred as well as a change in the relative abundance of the two species, with the mountain sucker now comprising a relatively small proportion of the population as compared to its 1951–52 levels.

In the limited distribution of the mountain sucker, habitat use almost completely overlaps that of the Tahoe sucker, and I was unable to document resource partitioning based on microhabitat preference. Although mountain suckers possess specialized morphological characteristics that seem adaptive to living and feeding in riffles and swifter current areas, they were never found in these habitats. The arrival of mountain suckers into the stream was, however, coincident with the increase in algae available on the substrate. Mountain suckers were observed feeding substantially more often than the associated Tahoe suckers. Sites with more algae were apparently selected by the mountain sucker, and this difference may reflect the presumed heavier use of diatoms and algae by the mountain sucker than by the Tahoe sucker (Hauser 1969, Marrin 1980). It seems unlikely, based on my observations, that the food resource in Sagehen Creek was limited or that one species prevented the other from feeding in an area, as both species were present at these sites and neither inter- nor intraspecific agonistic encounters were observed in the stream or stream observation tank. Resource partitioning was perhaps not evident because of the current low density of fishes and abundant algae.

The comparatively high degree of observed hybridization for the Lahontan Basin—13% reported by Flittner (1953) compared with 1% predicted by Hubbs et al. (1943)—indicated previously that isolating mechanisms may have been incomplete in Sagehen Creek. If former isolating mechanisms existed, such as segregation along a longitudinal gradient or on a microhabitat level, results of my study show that they may now be functionally nonexistent. To some extent, temporal segregation may limit the time of spatial overlap between the two suckers, as documented for other sympatric sucker species (Nelson 1968). Mountain suckers were absent when Tahoe suckers were spawning. A smaller size class (110–140 mm total length) of the Tahoe sucker, however, moved into the stream with similarly sized adult mountain suckers and was present and abundant at sites when mountain suckers appeared ready to spawn in mid-August. It is possible that the Tahoe suckers present were ripe, even though large Tahoe suckers (160–220 mm total length) had spawned earlier. The possibility also exists that the smaller Tahoe suckers moving into the stream with the mountain suckers were hybrids.

Distribution and abundance data from Sagehen Creek and three local streams show that populations of the mountain sucker are now extremely limited and suggest that species may have become vulnerable to local extinction; at best, mountain suckers are certainly rare in these areas. Similar shifts between years in relative abundance of suckers were not evident at the eastern Lahontan Basin sites in Nevada. The differences between regions are possibly due to an interaction of reduced and altered habitat and destructive management practices in the mountain sucker areas in eastern California.

In Sagehen Creek and three other nearby stream, the impoundment of reservoirs seems to have reduced the habitat area of the mountain sucker and may have eliminated former mechanisms isolating it from the Tahoe sucker. The inundation of lower Sagehen Creek may also have contributed to the Tahoe sucker overwhelming the mountain sucker in these areas, thereby increasing the probability of genetic swamping (Hubbs 1955).

The loss of a sucker species due to introgressive hybridization has been documented by Andreasen (1975). Although I have not determined whether the proportion of hybrids in the Sagehen Creek population has increased since 1951, it seems doubtful that a population of 40 individuals—down from 1,630 (Flittner 1953)—can persist much longer. In two years of observation, young-of-the-year mountain suckers were absent in Sagehen Creek and in the three other local streams. Such was not the case at the eastern Lahontan Basin sites in Nevada. It also seems unlikely that the reservoirs harbor large populations of the mountain sucker, since they have yet to be noted in collections by other researchers.

Acknowledgments

The research described here is based on my thesis presented to the Department of Forestry and Resource Management, University of California, Berkeley, in partial fulfillment of the requirements for the Master of Science degree. Financial support was in part from the University of California Agriculture Experiment Station, the Wildlife and Fisheries Graduate Student Fund, and the Paul R. Needham Fund. Living and laboratory facilities were provided at the Sagehen Creek Field Station during fieldwork portions of the study. Special thanks go to D. Erman for providing the opportunity as well as support and guidance during all phases of the research, and to P. Moyle who initially sparked my interest in native fishes. R. Miller generously provided copies of his field notes from early surveys of the Lahontan Basin. M. Brereton, V. Landrum, S. Martin, B. Wagner, M. Yoder-Williams, and M. P. Yoder-Williams helped with fieldwork. D. McCullough, L. Maxwell, P. Moyle, G. Nelson, M. Power, and an anonymous reviewer made helpful comments on various drafts of the manuscript.

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DIET SIMILARITY BETWEEN ELK AND DEER IN UTAH

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ABSTRACT.—Growing numbers of elk (*Cervus elaphus*) on winter ranges might adversely affect sympatric wintering mule deer (*Odocoileus hemionus*) if diets of the two species are similar. Diets of elk and deer on a northern Utah range were analyzed for overlap in winter with microhistological analysis of fecal samples. Diets overlapped 71%. No significant difference was found in use of grasses or shrubs between elk and deer; however, use of forbs was significantly different. Shrubs comprised the largest proportion of the diets of both elk and deer. Deer might be under more severe dietary stress than elk on poor winter ranges.

With near extirpation of Rocky Mountain elk in Utah at the turn of the century, mule deer became the dominant wild ungulate (Bryant and Maser 1982). In 1912–1915 elk were reintroduced in Utah with transplanted animals from Jackson, Wyoming. Since then, elk populations have been increasing as a result of sound management practices.

Historically, wintering deer moved to low elevations on valley floors and bordering foothills. Residential, industrial, and commercial development of valleys and bench areas of the Wasatch Front in Utah has restricted mule deer from wintering on ranges to which they were historically accustomed. In the mountainous foothills northeast of Springville, Utah Co., Utah, deer have recently been subjected to another impingement. A herd of elk immigrated onto this very localized range about 20 years ago to winter on the south-facing slopes. The herd has returned annually and now numbers approximately 100 animals.

Before more specific studies provided evidence to the contrary, elk and deer were often classified as grazers and browsers, respectively (DeNio 1938, Gaffney 1941, Cowan 1947). More recent studies have shown that elk and deer diets overlap on occasion (Morris and Schwartz 1957, Mackie 1970, Hansen and Reid 1975). During nonstressful periods, partitioning of food and space occurs; deer use browse and forb species and elk use a preponderance of grass and forb species in separate vegetative communities (Kufeld 1973, Hobbs et al. 1979, Collins and Urness 1983). During periods of snow cover and other limited grazing conditions, both elk and deer can subsist on browse species alone (Cliff 1939, Gaffney 1941, Cowan 1947). The steep slopes of the hills near Springville are dominated by oak-maple-shrub communities interspersed with annual and perennial forbs and grasses (Swenson et al. 1972). The objective of this study was to obtain quantitative measures of association between species and similarity between diets of wintering elk and deer.

METHODS

Dietary composition was determined from microhistological analysis of plant epidermal fragments remaining in feces. From January through March 1983, fecal pellets of elk and deer were collected from the study site only on areas where elk had been observed the same day or a few days earlier to guarantee freshness. Three to five pellets were collected from each defecation of both elk and deer. Sample pellets were collected from several pellet groups across the entire area where animals had been observed to ensure that no individual animal was overrepresented. Ten or more pellet groups were sampled at each area. Pellets were put into plastic bags and frozen until time of processing.

In fall 1983, plants were identified and collected on the study site in quantities sufficient both to press for voucher specimens and to process for tissue reference slides. Reference and test slides were prepared as outlined by Vavra and Holechek (1980). Slides were permanently set in Naphrax High Resolution Diatom Mountant (Northern Biological

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Supplies, Ipswich, England). A 90% accuracy level in identifying epidermal tissue was achieved through training (Holechek and Gross 1982) prior to reading slides of fecal material.

Fecal material was cleared in a solution of 1:2 chlorine bleach and water but otherwise prepared and mounted in the same manner as reference material (Holechek 1982). Chlorine bleach cleared fecal pigments faster than did 0.05M NaOH. A total of 30 slides, 20 fields per slide, were read for each species, representing more than 60 elk defecations and more than 30 deer defecations. Percent frequency was calculated from frequency of occurrence of each plant species identified on slides. Percent frequencies were converted to densities, and from densities to relative densities, which reflect relative amounts of each plant eaten (Todd and Hansen 1973). Overall diet similarity for shared forages was calculated from percent relative densities with the Gauch formula (Gauch 1973, Hansen and Reid 1975). Overlap within each individual forage moiety (grasses, forbs, or shrubs) was also calculated.

Results

Overall diet similarity was 71% among common forage species comprising elk and deer diets. Some relative underestimation of elk use of shrubs might be inherent because elk can browse larger leaders than deer can, which decreases ingested mass in relation to epidermal surface (Gill et al. 1983). Elk and deer diets were 80% similar in shrub species, 49% similar in forbs, and 65% similar in grasses (Fig. 1). Relative densities of each forage moiety in elk diets were 61% shrubs, 6% forbs, and 33% grasses. Relative densities in deer diets were 57% shrubs, 15% forbs, and 28% grasses (Fig. 2).

Forage moieties were significantly associated with elk and deer ($P < .001$) when frequency of occurrence was analyzed in two-way contingency tables. However, when contribution of forbs to the association was removed, shrub and grass use was not significantly different between elk and deer (alpha = .01). Thus, elk and deer diets differed primarily in forb composition, but forbs were the smallest relative contributor to the diets of elk and deer (Fig. 2).

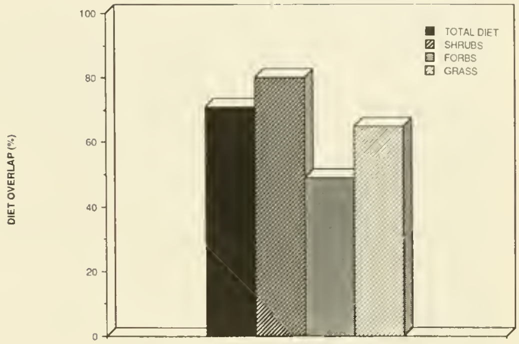

Fig. 1. Percent overlap of entire diet and each forage type for wintering elk and mule deer in Utah, 1983.

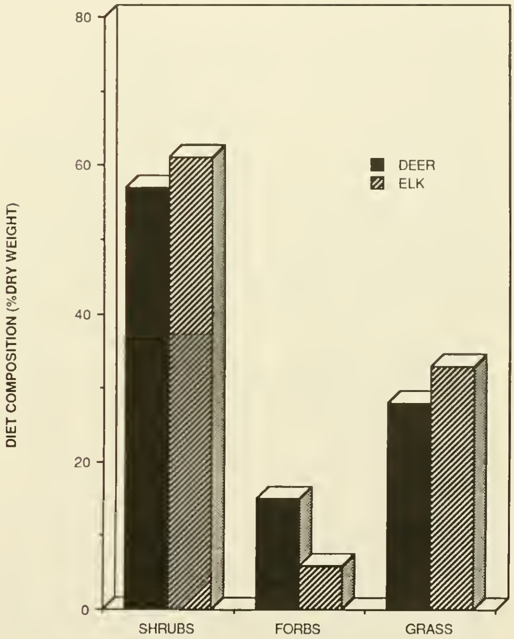

Fig. 2. Dry weight percentage of total diet each forage type contributes to wintering elk and mule deer in Utah, 1983.

Both elk and deer relied largely on shrubs, particularly on gambel oak (*Quercus gambelii*) and sumac (*Rhus* spp.) (Table 1). Both smooth sumac (*R. glabra*) and skunkbrush sumac (*R. trilobata*) were present on the site but could not be discerned separately by epidermal characteristics. Smooth sumac was probably the greater contributor to diets because it was much more abundant. All stands of smooth sumac observed were severely damaged from extensive winter browsing and trampling. Cheatgrass (*Bromus tectorum*)

TABLE 1. Percent relative densities of plant species discerned in feces of elk and mule deer in Utah, 1983.

Forage species	Relative density	
	Elk	Deer
Shrubs		
Acer grandidentatum	9	8
Artemisia tridentata	1	1
Cercocarpus ledifolius	3	<1
Cercocarpus montanus	<1	–
Chrysothamnus nauseosus	–	4
Cowania mexicana	3	3
Quercus gambelii	69	51
Rhus spp.	16	33
Forbs		
Artemisia ludoviciana	6	2
Aster chilensis	21	11
Astragalus utahensis	–	3
Epilobuim canum	–	3
Erigeron divergens	2	1
Eriogonum spp.	5	–
Erodium cicutarium	5	5
Helianthus annuus	13	48
Heterotheca villosa	6	17
Linum lewisii	6	1
Marrubium vulgare	–	3
Oenothera caespitosa	21	3
Petradoria pumilla	–	1
Physalis longifolia	6	–
Xanthocephalum sarothrae	9	3
Grasses		
Agropyron cristatum	15	5
Agropyron intermedium	26	16
Agropyron spicatum	16	7
Aristida purpurea	7	2
Bromus tectorum	14	38
Poa bulbosa	20	31
Sporobolus cryptandrus	1	–

dominated grass species found in the diet of deer, but elk used a variety of grasses (Table 1). Deer also consumed more forbs, especially sunflower (*Helianthus annuus*), than did elk.

Mule deer had a slightly more diverse diet than elk. Deer had a Shannon-Wiener diversity index of 2.33, whereas elk had an index of 2.03.

Overall there was a high similarity (71%) in diets of elk and deer, with little separation in types of forages selected. Forages consumed by elk and deer were of low quality and diversity. Both elk and deer relied most heavily on shrub species, but deer consumed more forbs than did elk. Available forbs were mostly dead, leached annuals from the previous season's growth. Many of the species found in diets of deer are those typical of lower regions of foothills, such as sunflower and cheatgrass.

DISCUSSION

Elk and deer diets overlapped on this winter range for two reasons: (1) vegetative diversity was low, and (2) availability of forbs and grasses was reduced in winter by plant dormancy and snowcover. Elk and deer were forced to select similar forages because availability and choice of forage species were both limited.

We believe that conditions on this range caused competition between wintering elk and deer, but further sampling of snow depth, plant phenology, plant availability, and amount of available forage should be done to define parameters of competition that might exist. If diet overlap is sufficiently extensive and food resources are sufficiently limited and in short supply, resource partitioning must occur in time or space. Nonquantified observations indicate this is true at least for space.

Severe damage caused by deer browsing fruit and ornamental trees is common in areas of Springville and surrounding fields and suburbs. It appears that part of the reason deer are in such close contact with humans is that larger elk on bench areas browse to a level in the shrub canopy that is too high for deer to reach (Rounds 1979). Larger body size allows elk to high-line available browse, move with greater ease than deer do through deep snow (Parker et al. 1984), and directly interfere with deer groupings (Jenkins 1988). The latter was observed on several occasions. Elk are also able to browse shrub and tree leaders with larger diameters, leaving terminals that are too large in diameter for deer to eat.

Larger species typically have greater diversity in prey size and species selection under normal conditions (Mackie 1970, Schoener 1971), but in our study, deer diets were equally diverse or slightly more diverse than elk diets. Since diet diversity often increases under conditions of food resource shortages (Gullion 1966), mule deer probably selected more feeds because they were under dietary stress. Under more favorable conditions deer might have had a less diverse and more specialized diet.

While sampling, we observed dogs, hikers, cross-country skiers, snowmobilers, motorcyclists, and all-terrain vehiclists disturbing wintering animals. Human disturbance during periods of winter stress and poor forage conditions may further reduce survival of wintering elk and deer (Parker et al. 1984). Clearly, further research is needed to more adequately define any competitive interaction between elk and deer; however, managers must be prepared to adjust carrying capacities of one or both species if reduced vigor becomes increasingly manifest in populations in winter.

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EFFECT OF INDOMETHACIN-TREATED WHEAT ON A WILD POPULATION OF MONTANE VOLES

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ABSTRACT.—Semiweekly mark and recapture livetrapping was conducted July–October 1985 to determine the effectiveness of wheat treated with indomethacin, a prostaglandin synthetase inhibitor, to control the productivity of a wild population of montane voles (*Microtus montanus*) in southeastern Idaho. Before treatment, control (C) and experimental (E) groups, each on ca 0.3 ha, were statistically equal in population size ($\bar{x}$ ± SD; C = 50 ± 21, E = 45 ± 14), adult female:male ratio (C = 1:0.8, E = 1:0.7), juvenile:adult ratio (C = 0.16:1, E = 0.13:1), number of juveniles per 100 females ($\bar{x}$ ± SD; C = 27 ± 8, E = 21 ± 18), and percentage of pregnant females ($\bar{x}$ ± SD; C = 44 ± 10, E = 46 ± 17). After the 15-week experiment all population categories were unchanged for the control group and significantly ($P \leq .05$) lower for the experimental group, which ended with a final population of ($\bar{x}$ ± SD) 17 ± 6, with 7 ± 21 juveniles per 100 females and an 11 ± 14% pregnancy rate.

The peak phase of most cyclic microtine populations is relatively short in duration (Krebs et al. 1973) but can result in dramatic changes in habitat (Freeland 1974, Summerhayes 1941, and others). These changes are especially obvious and troublesome when the rodents infest economically or aesthetically valuable lands. At such times the offending rodent species generally is considered a pest, and efforts are usually made to reduce the population by various lethal biological, mechanical, and/or chemical control methods (Byers 1985).

Many nonlethal compounds have been tested as chemosterilants to regulate productivity in pest rodent species. Most of these compounds are natural or synthetic estrogens, progestins, and steroids or their derivatives (e.g., Andrews et al. 1974, Austin and Bruce 1956, Brooks and Bowerman 1971, Dziuk 1960, Gwynn 1972a, 1972b, Gwynn and Kurtz 1970, Howard and Marsh 1969, Kendle et al. 1973, Kincl and Dorfman 1965, Kincl et al. 1965, Marsh and Howard 1969, Mischler et al. 1971, Storm and Sanderson 1970). Some of the compounds successfully reduced fecundity of pest species. But, because of bait aversion and/or short duration of action, these are not routinely used for widespread rodent control (German 1985).

Prostaglandin synthetase inhibitors are a group of compounds that can prolong gestation (Liggins et al. 1973), inhibit ovulation (Armstrong and Grinwich 1972, Bowring et al. 1974, Diaz-Infante et al. 1974, Wallach et al. 1975), and reduce the release of gonadotropin-releasing hormone from the hypothalamus (Chobsieng et al. 1975, Ojeda et al. 1979). Indomethacin is a nonsteroidal, analgesic compound that inhibits prostaglandin synthesis. It is recognized as a relatively nontoxic compound that can effectively inhibit reproduction in wild and captive populations of deer mice, *Peromyscus maniculatus* (Seeley 1983). The effect of indomethacin on reproduction in wild populations of other rodent species has not been previously studied. The objective of this study was to determine the effect of indomethacin-treated wheat on the reproduction and survival of a wild population of montane voles (*Microtus montanus*) in southeastern Idaho.

MATERIALS AND METHODS

The study was conducted about 65 km NNW of Pocatello, Bannock Co., Idaho, on the U.S. Department of Energy's Idaho National Engineering Laboratory (INEL). Fieldwork was performed 14 July–25 October 1985 on nearly equal-sized control and experimental plots (ca 0.33 ha) about 450 m apart and separated by several roadways and rows of buildings. Both plots were portions of cultivated lawns, dominated by *Poa* spp., that were mowed weekly and irrigated daily until mid-September. Lawns were surrounded by pavement or buildings, with each separated from native sagebrush-grassland vegetation by a roadway on one side only. At the onset of the study the vole population on the INEL was in the second year of high-population density. The sitewide population subsequently crashed during the 1986–87 winter (B. L. Keller, Idaho State University, personal communication; T. D. Reynolds, unpublished data).

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Longworth live traps were employed simultaneously on both plots, 86 on the control area and 84 on the experimental plot. The trapping matrices were relatively small because of limited usable lawn space. Traps were placed approximately 3 m apart adjacent to rows of aboveground irrigation pipe separated by about 5 m. Traps were generally located near active vole burrow openings and runways that were common within 0.5 m of the irrigation pipe. Traps were set two evenings weekly (Sunday and Wednesday) and checked the following mornings. Traps were either locked open or, to accommodate the lawn maintenance crew, removed from the study area between trapping sessions. Approximately 20–30 g of whole wheat was maintained as bait in traps on the control area throughout the study. Additional wheat was scattered near the trap sites. In the experimental area, untreated wheat was placed in the traps for the first two weeks (four trapping sessions) to familiarize the animals with the novel food source. Indomethacin-treated wheat was then placed in and near the experimental traps for the remainder of the study. Wheat was treated by dissolving 10 grams of indomethacin[3] (Sigma Chemical Co., St. Louis, Missouri) in 300 ml acetone and stirring the mixture into 3.5 kg whole wheat until the acetone evaporated. The indomethacin appeared evenly distributed as a white powder on the grains of wheat at the original concentration of about 0.29% indomethacin (2.9 g/kg wheat).

The sex and age (adult or juvenile) were determined and recorded for all voles captured. The reproductive condition of females (pregnant or not) was also recorded. Voles weighing ≥ 20.0 g were considered adults. Numbered fingerling tags were placed in one ear of each newly captured vole prior to release at the point of capture. At the end of the study the minimum population (number of voles known alive), including individual tallies of adult and juvenile male and female voles, was enumerated (Krebs 1966) for each trapping session. Because the time required for the effects (if any) of indomethacin on productivity to be measurable was unknown, data were divided into three periods of 10 trapping sessions (five weeks) each for analysis. We did not know how much indomethacin-treated wheat each animal would consume. But, based on Seeley's (1983) data for deer mice, we concluded that experimental animals would receive an effective dose of indomethacin in less than three weeks. Because we baited with untreated wheat during the four initial trap sessions (two weeks), the first five weeks of the study thus provided the initial population data for both study areas and was called the Baseline period. The second 10-trap session (five weeks) constituted a Transition period. Productivity and/or survivability of some, but not necessarily all, voles might have been influenced by the drug during this period. Therefore, although means for the Transition period were calculated to document trends, these data were omitted from statistical analyses. If it took three weeks for the indomethacin-treated wheat to reduce fertility or inhibit ovulation, it would take about five more weeks (the gestation plus the preweaning period of montane voles; Bailey 1924, Hoffmann 1958, Jannett 1978) before effects of indomethacin, as determined by the number of juveniles entering the trappable population, could be measured with confidence. We therefore called the final 10-trap session the Effect period.

Because little is known about the effects of indomethacin on wild rodent populations, we analyzed our data with several objectives. We felt that examining both absolute and relative (% of the total number of animals) abundances of subsets (e.g., F, M, ad, and juv) of the control and experimental populations would best elucidate the specific portions of the populations affected by the drug. The minimum population was analyzed with a two-way analysis of variance followed by Student-Newman-Keuls Multiple Range Test (Zar 1984). Time period (Baseline and Effect) and treatment (with or without indomethacin-treated wheat) were the independent variables. Similar tests were performed for the relative number (%) and minimum number known alive of the subsets composed of adult males, adult females, and juveniles, as well as the percent of the females that were pregnant and the number of juveniles captured per 100 adult females. Because percentages and proportions form a bimodal rather than a normal distribution (Zar 1984), an arcsine transformation (Freeman and Tukey 1950) was performed before comparing all percentage data. Moreover, outlying data points were identified and omitted from analysis following the methods of Dixon (1950). A level of significance of $P < .05$ was selected for rejection of all hypotheses.

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[3] Use of trade names and supplies does not imply endorsement of commercial products.

RESULTS

The two-way ANOVA yielded significant interaction effects ($P \geq .05$) for all comparisons between subsets of the two study groups except the number of adult males known alive, juveniles known alive, and juveniles per 100 females. For each of these population subsets the simple (main) effect of treatment was significant for comparisons between groups. Because there were only two levels of treatment, a follow-up test was not needed (Cody and Smith 1987) to conclude that there were fewer adult males, juveniles, and juveniles per 100 females after indomethacin-treated wheat was provided to the experimental group. Significant interaction for the other comparison indicated that either the simple effect of treatment or the simple effect of time period was different between groups for each subset. Main effects of treatment and time period were both significant for all remaining comparisons. Because the expression of treatment effects is coupled to a change in time period, these results indicate a significant change in all subsets of the treatment group between the beginning and the end of the study.

All population parameters for the control group were no different at the end of the study than at the beginning, while all parameters for the experimental group were significantly different between Baseline and Effect periods (Table 1).

The control group experienced a slight increase in the total number of animals known alive during the Transition period. The number of adult males and females known alive in the control group remained constant throughout the study, while fluctuations in the number of juveniles within the control group paralleled the population fluctuations. The relative number of males, females, and juveniles in the control population remained relatively constant at about 38:48:14 throughout the study. The proportion of females that were pregnant and the number of juveniles per adult female were also constant over the study.

The total number of animals known alive in the experimental group remained relatively stable during the Baseline and Transition periods, declining significantly in the Effect period (Table 1). The number of males declined by about 25% over the study, while the number of females declined about 80%. Juvenile numbers declined nearly 90%. The proportion of males, females, and juveniles in the experimental group fluctuated significantly from an initial ratio of 37:53:10 to a final ratio of 68:31:1. The proportion of pregnant females successively declined throughout the study. The number of juveniles per 100 adult females was significantly lower during the Effect period.

The control and experimental populations, although the same in all respects at the beginning of the study, differed in all respects at the end of the study (Table 1). The two indices of productivity, the proportion of adult females that were pregnant and the number of juveniles per 100 adult females, were both significantly greater in the control than in the experimental group in the Effect period.

DISCUSSION

The experimental and control groups were equal for all parameters examined during the Baseline period. Thereafter the population structure and dynamics of the two groups differed. We have no data to suggest that subsequent differences were the result of inherent group differences in demography, physiology, or predation. Considering the proximity of the study groups to each other and the

TABLE 1. Effects of indomethacin-treated wheat on montane voles. Means (± SD) are for five-week (10-trap session) Baseline, Transition, and Effect periods, calculated from minimum number known alive enumerations for each population subset.

Subset	Baseline		Transition[1]		Effect	
Minimum number of voles						
Control	50.4	(20.6)A[2]	61.4	(4.5)	44.4	(7.3)A*[3]
Experimental	44.6	(14.4)A	41.9	(6.1)	17.3	(6.1)B*
Minimum number of adult males						
Control	17.7	(7.6)A	23.7	(2.8)	18.9	(5.1)A*
Experimental	15.9	(4.4)A	17.7	(1.4)	11.4	(2.8)B*
Relative number of adult males (%)						
Control	34.5	(3.5)A	38.8	(5.5)	41.8	(5.9)A*
Experimental	36.8	(5.8)A	43.0	(6.6)	67.6	(7.4)B*
Minimum number of adult females						
Control	26.0	(10.9)A	27.7	(1.6)	21.0	(2.5)A*
Experimental	23.7	(8.7)A	16.2	(2.4)	5.6	(3.4)B*
Relative number of adult females (%)						
Control	51.6	(4.6)A	45.3	(4.1)	47.8	(4.7)A*
Experimental	52.7	(5.5)A	39.1	(6.0)	30.6	(7.3)B*
Minimum number of juveniles						
Control	6.7	(2.8)A	10.0	(5.9)	4.5	(1.2)A*
Experimental	5.0	(3.6)A	8.0	(5.4)	0.3	(0.7)B*
Relative number of juveniles (%)						
Control	13.8	(3.2)A	15.9	(8.3)	10.3	(2.8)A*
Experimental	10.4	(7.8)A	17.9	(11.1)	1.7	(4.5)B*
Proportion (%) of pregnant adult females						
Control	44.5	(10.3)A	38.3	(13.2)	34.9	(10.3)A*
Experimental	46.5	(16.8)A	26.4	(15.4)	11.2	(13.7)B*
Number of juveniles per 100 adult females						
Control	27.3	(8.3)A	36.6	(22.0)	21.2	(6.0)A*
Experimental	21.1	(18.2)A	50.2	(35.2)	7.3	(21.0)B*

[1] Transition period data not included in statistical analyses.

[2] Means in a row followed by the same letter are equal ($P > .05$).

[3] Means in a column of a couplet followed by an asterisk are different ($P < .05$).

similarity of habitats, such differences would be highly unlikely. Although the study areas were too distant to allow an exchange of individuals (no marked animals from one area were ever recaptured in the other), the groups were most certainly part of the same local deme. Therefore, we are confident that our analyses indeed assessed the impacts of the indomethacin treatment.

During the Effect period the experimental population was significantly smaller than the control. This was the result of a significant decrease in the minimum number known alive of all population subsets: adult males, adult females, and juveniles. These data suggest that indomethacin-treated wheat can be effective in reducing a population of montane voles. This was likely the result of both indomethacin-induced mortality and changes in reproductive potential within the experimental group. Some toxic and debilitating effects of indomethacin are reported (Lee et al. 1971), and we did find about a dozen morbid voles on the experimental site early in the study. But, our data also indirectly and directly demonstrate a reduction in productivity by the experimental group. Notably, juvenile recruitment during the Effect period, as measured by the relative number of juveniles known alive in each population, was significantly less in the experimental group (1.7 ± 4.5%) than in the control group (10.3 ± 2.8%). And, more directly, the experimental group was significantly less than the control for the two productivity indices: the percentage of females that were pregnant (C = 34.9 ± 10.3%; E = 11.2 ± 13.7%) and the number of juveniles per 100 females (C = 21.2 ± 6.0; E = 7.3 ± 21.0). This mean number of juveniles per 100 females for the experimental group includes the only data point that was determined to be an outlier. During the first trapping session of the Effect period 1 juvenile and 16 adult females (ratio of 7%) were captured on the experimental site. No juveniles were captured during the following eight trapping sessions (four weeks). The last trapping session yielded 2 juveniles and only

3 adult females (67%), clearly a misleading ratio. When the outlier was omitted, as it was for the statistical comparisons, the average number of juveniles per 100 females was only 0.8 ± 2.4. Although it is possible that after eight weeks with no juveniles entering the experimental population, two were produced, it is likely that these two individuals were immigrants from surrounding areas dispersing into the sparsely occupied experimental site during the Effect period. The closest suitable habitat was ca 100 m from the experimental site.

Differences over time within each study group demonstrated group trends in population dynamics. The slight changes in the minimum number of voles known alive within the control group most likely represented normal, annual population fluctuations (Johnson 1987). Fluctuations in our data for juveniles mimic the control group as a whole and indicate that control population changes resulted from differences in the number of juveniles entering the control population.

The experimental group followed a different pattern. The number of juveniles entering the population never increased and, in fact, decreased significantly during the Effect period. The number of females known alive, the proportion of females, and the percentage of pregnant females within the experimental group decreased from one study period to the next. The number of adult males known alive declined only in the Effect period, although the proportion of the experimental group represented by adult males increased. This suggests that females in general, and pregnant females in particular, may have been less resistant to any toxic effects of the indomethacin-treated wheat than males. The significant decrease within the experimental group of juveniles per 100 adult females during the Effect period does not indicate whether this was the result of decreased fecundity of individual females or fewer gravid females in the population.

Regardless of the mechanism, productivity and recruitment in the experimental group were significantly less than in the control group. The steady and significant decrease in the proportion of pregnant females in the experimental group, coupled with the decreased number of juveniles per adult female, suggests that indomethacin-treated wheat can reduce both the incidence of pregnancy and individual reproductive output of montane voles and consequently reduce population levels substantially. We conclude that differences within the control population (e.g., slight increase followed by significant decrease in total population and juveniles) represented normal annual population changes (Johnson 1987), while differences between the groups and within the experimental group were the result of the latter feeding on indomethacin-treated wheat.

This study was not designed to test vole acceptance or avoidance of bait treated with indomethacin. However, the steady decline over nearly four months observed in the experimental group strongly suggests that animals were not avoiding the treated bait. Biweekly baiting with indomethacin-treated wheat throughout the experiment was part of our study design. Using indomethacin-treated wheat to control other populations of montane voles may be neither time nor energy efficient. Whether less frequent applications of the treated wheat would produce similar results is unknown. Among other legal and biological considerations, dose rates and effects on nontarget species need to be investigated before indomethacin could be legitimately considered an effective rodent-control agent. The results of our research indicate that additional studies are warranted.

Acknowledgments

Funds for this study were provided by the Landlord Account, administered by EG&G Idaho, Inc., for the Idaho Operations Office of the U.S. Department of Energy. M. H. and R. R. Schabacker's commitment to the fieldwork of this study is gratefully acknowledged. We thank J. W. Laundré and B. L. Keller for their valuable suggestions regarding statistical analyses, and O. D. Markham and R. E. Marsh for their constructive reviews of the draft manuscript. This is a contribution from the Idaho National Engineering Laboratory Radioecology and Ecology Program.

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LITTER DECOMPOSITION BY ARTHROPODS IN UNDISTURBED AND INTENSIVELY MANAGED MOUNTAIN BRUSH HABITATS

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ABSTRACT.—The population dynamics and decomposition activities of litter arthropods in an unmanaged sagebrush/bitterbrush habitat in southeastern Wyoming were assessed in 1986. The effects of sagebrush/bitterbrush management practices on litter arthropod communities and the role of these communities in decomposition were also assessed. Insecticide applications were used to selectively exclude arthropods in order to determine the ecological impact of these detritivores. Application of a herbicide, 2,4-D, was associated with increased arthropod populations for 30 days following treatment. Mowing increased arthropod densities at two different times, 10–30 days and 50 days posttreatment, perhaps as a result of functional and numerical responses by litter arthropods. Elimination of arthropods from otherwise undisturbed shrub habitats by the use of broad-spectrum insecticides reduced the rate of litter decomposition during the growing season, indicating that these organisms play an important role in decomposition and nutrient cycling.

Sagebrush (*Artemisia* spp.)-dominated lands of the western United States cover more than 100 million ha (Beetle 1960). Sagebrush is considerably less palatable to domestic animals than are many other range shrubs (Powell 1970). Consequently, burning, herbicide applications, and mowing are widely used in an attempt to reduce densities of this plant (Powell 1970). While it is apparent that such disturbances in sagebrush communities enable economically more desirable grasses to populate range areas, little is known regarding the impact on arthropod populations and the resultant effects on decomposition and nutrient cycling.

Many studies have shown that habitat disturbance influences arthropod densities, species distribution, and community diversity of grassland ecosystems (Blocker et al. 1971, McDaniel 1971, Morris 1971, Lavigne and Kumar 1974, Kumar et al. 1976). Although virtually nothing is known concerning the role of arthropods in the ecology of sagebrush/bitterbrush habitats, studies of other ecosystems have shown that during disturbance and succession, changes in the types and abundance of plants and the associated litter affect arthropod diversities (Murdoch et al. 1972, Southwood et al. 1979).

Studies of litter decomposition have been conducted in undisturbed ecosystems including desert, prairie, and forest but not in sagebrush/bitterbrush habitats. Several studies (Strojan et al. 1987, Schaefer et al. 1987, Whitford et al. 1986) have revealed either short- or long-term correlations of rainfall with litter decomposition in desert habitats. However, Schaefer (1985) showed that organic matter, but not moisture, affected litter fauna. Other studies (Santos et al. 1984, Santos and Whitford 1981) on desert habitats used a single application of chlorodane to individual litter bags to demonstrate that litter decomposition declines by 24–53% in the absence of arthropods. Vasobrinch et al. (1979) found that soil mites, microbial activity, and rainfall increased decomposition in shortgrass prairie.

The objectives of this study were to determine the effects of intensive mountain shrub management practices on populations of decomposer arthropods and to ascertain the role of these arthropods in litter decomposition throughout a season.

MATERIALS AND METHODS

This study was conducted on a sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*) habitat located at an elevation of 2,400 m, 12 km southeast of Saratoga, Carbon County, Wyoming. Soils are of the North Park Formation of brown, sandy loams developed on loess, limestone, sandstone, and tuff. Rainfall and temperature were recorded throughout the study period. The study area averages 480 mm precipitation per year, with most of the moisture being provided by snow; 102 mm of rainfall was measured during the study period. The mean annual temperature is 10.2 C, and temperatures ranged from 21.0 to 27.0 C during the study period.

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Within the study site, twelve 4-ha blocks were randomly chosen from areas that had similar vegetation and soil characteristics. Habitat manipulation consisted of mowing four blocks to a 20-cm stubble height or applying 2,4-D butyl ester in water at a rate of 0.91 kg per acre to four blocks in May of 1986. Four blocks were left untreated to be used as control plots.

Two insecticides, carbaryl (1.68 kg/ha) and malathion (1.4 kg/ha), were alternately applied every two weeks to half of each treatment and control block. The other halves of the blocks were left unsprayed and served as controls for comparison of litter decomposition. These broad-spectrum insecticides provided a reduction in the total arthropod population. By using half-blocks (2 ha) as the smallest units of treatment plots, we reduced migration of arthropods into and around litter bags; this prevented feeding before the insecticide could affect arthropods, a potential problem with treated litter bags.

Ten nylon litter bags, 15 × 15 cm with 1.5-mm mesh, were filled with 20 g of ground litter (Webb 1977) from each site. They were then placed in open (sagebrush-free) and closed (sagebrush-canopied) areas within each half-block (insecticide treated and untreated) in the last week of May 1987. The litter bags were collected the first week of September 1987 and weighed to determine the amount of decomposition. The total decomposition period studied was 100 days.

Litter decomposition rates were also determined by collecting twenty 0.5-m^2 samples of litter from each of the insecticide-treated and untreated half-blocks. Arthropod densities were determined by collecting eighty 0.25-m^2 plots of litter from each half-block every 10 days throughout the study period. Arthropods were separated from litter material in the laboratory by Berelese funnels.

Differences in arthropod densities following application of herbicide and differences in litter biomass and rate of decomposition by mowing were analyzed by ANOVA and a least significant difference post-ANOVA test. Correlations of rainfall, temperature, and arthropod densities with litter decomposition were calculated with step-wise regression. Chi-square was used to determine management practices on total canopy cover.

RESULTS AND DISCUSSION

Litter Production and Decomposition

There was no significant ($P > .10$) linear correlation of rainfall ($r^2 = .42$) or temperature ($r^2 = .38$) with litter decomposition. Because the growing season (May through September) is short, dry, and has fairly constant temperatures, this is not a surprising result.

Litter biomass remained virtually constant in control plots throughout the course of the study. Mowing increased the litter biomass by 6.4-fold, and herbicide application increased litter biomass by 3.0-fold. Since there may be a delay of a year or more before sagebrush leaves drop in herbicide-treated areas, these results may underestimate long-term litter biomass production for the latter treatment.

Brush management practices reduced the canopy cover of treated blocks, while unmanaged blocks showed no change in shrub canopy cover. There was a 40.9% decrease in shrub cover in herbicide-treated blocks and a 24.1% decrease in shrub cover in mowed blocks (Table 1).

Litter decomposition for this study area ranged from 24% to 53% for the 100-day period, depending on the brush management strategy and insecticide treatment (Table 2). Differences in decomposition in litter bags as a function of management and treatment were reflected in the loose litter samples (Table 3). Decomposition rates in undisturbed areas were comparable to the 51–68% losses per growing season found on sites in Idaho (Murray 1975), 50% litter decomposition in an area of Washington (Mack 1977), and decomposition losses of 43–53% near Reno, Nevada (Comanor and Staffeldt 1978).

Effects of Shrub Management on Litter Arthropods

Acari, Collembola, and Thysanuran populations (Table 4) fluctuated throughout the first 50 days and then remained relatively constant for the remaining 50 days of the study

TABLE 1. Effects of brush management practices on percent canopy cover.

Treatment	Year[a] 1985	1986
Unmanaged	28.1a	28.1a
Herbicide	29.6a	17.5b
Mowed	31.6a	24.0b

[a] Means for a parameter followed by different letters differ significantly between years ($P < .05$; chi-square). N = 60.

TABLE 2. Effects of shrub management and insecticide treatments on percent decomposition in litter bags in a mountain brush habitat.

		Management practice[a]		
Habitat	Insecticide	None	Mow	Herbicide
Open	Present	32.9Aa	50.8Ba	28.7Aa
	Absent	53.0Ab	23.5Bb	37.6Ab
Covered	Present	29.0Aa	47.6Ba	51.0Ba
	Absent	53.0Ab	51.2Aa	44.8Aa

[a] Litter biomass means across insecticide treatments and within habitats and management practices followed by different lower-case letters differ significantly ($P < .05$). Litter biomass means across management practices within the same habitat and insecticide treatment followed by different upper-case letters differ significantly ($P < .05$).

TABLE 3. Effects of shrub management and insecticide treatments on litter biomass ($g/0.5m^2$) in a mountain brush habitat.

		Management practice[a]		
Habitat	Insecticide	None	Mow	Herbicide
Open	Present	17.9Aa	23.5Aa	65.1Ba
	Absent	8.8Ab	56.2Bb	25.9Cb
Covered	Present	135.3Aa	74.4Ba	82.6Ba
	Absent	7.7Ab	56.6Ba	101.5Ca

[a] Litter biomass means across insecticide treatments and within habitats and management practices followed by different lower-case letters differ significantly ($P < .05$). Litter biomass means across management practices and within the same habitat and insecticide treatments followed by different upper-case letters differ significantly ($P < .05$).

(Figs. 1–4). Mite densities were usually lower in open areas (i.e., intershrub spaces) than in closed areas (i.e., under shrub canopy). But Collembola densities were nearly the same in litter in open areas as in closed areas or somewhat higher.

The herbicide treatment increased ($P < .05$) the abundance of litter arthropods for 30 days in both open and canopy-covered plots following treatment (Figs. 1–4). Because complete leaf drop following herbicide treatments is often delayed for a year or more, litter production may not solely account for the changes in arthropod abundance. The increase in abundance was primarily due to fungivorous mites. Degradation of 2,4-D increases fungal growth (Klingman et al. 1982), and this could increase the population density of litter decomposers (e.g., fungivorous mites and springtails). Since 2,4-D may degrade within two weeks of application (Meister 1987), the timing of the observed increase in arthropod populations is consistent with the indirect consequences of herbicide degradation. Corresponding to the increased populations of litter arthropods in herbicide-treated plots was a noticeable ($P < .10$) increase in litter decomposition rate. After 30 days, the arthropod population densities in herbicide and control areas did not differ greatly ($P > .10$); thus, the effect of 2,4-D on arthropod decomposers was apparently short-lived.

Mowing shrubs significantly increased ($P < .05$) litter arthropod populations for 30 days following treatment (Figs. 1–4). There was a significant increase ($P < .05$) in the population 40–50 days posttreatment, as well. The initial increase in arthropods was probably a result of immigration due to the sudden increase in resource (litter) availability. This type of immediate increase as a result of changes in the behavior of organisms has been termed a functional response in discussions of predator-prey dynamics (Price 1975). The later population explosion may have been a result of an increase in reproduction supported by an abundance of resources (litter). This type of time-lagged increase as a result of enhanced reproduction of the organisms has been termed a numerical response (Price 1975). Interestingly, the increases in litter arthropod populations were not clearly associated with an increase in litter decomposition.

Effects of Arthropods on Litter Decomposition

Insecticide application decreased litter detritivores by 78% in unmanaged blocks and 76% in mowed and herbicide treated-blocks (Table 5). The application of carbaryl and malathion on mowed, herbicide-treated, and undisturbed plots generally decreased litter decomposition (Tables 2, 3). Litter decomposition in undisturbed plots significantly decreased ($P < .05$) in both open and closed areas following insecticide treatments. Thus, litter arthropods appear to have an important role in litter decomposition in undisturbed sagebrush habitats. Coinciding with results of our study, Barret (1968) reported a large

TABLE 4. Impact of mountain brush management practices on density (no./sample) of litter arthropods in unmanaged (U), mowed (M), and herbicide-treated (H) plots.

Taxon	Time posttreatment[a]											
	0 days			10 days			20 days			50 days		
Habitat	U	M	H	U	M	H	U	M	H	U	M	H
COLLEMBOLA												
Orchesella hexfasciata Harvey												
Open	1a	2a	1a	1a	8a	7a	2a	56b	7a	1a	33b	29b
Closed	1a	1a	1a	1a	8b	8b	1a	9b	7b	1a	74b	39c
Isotoma viridis (Bourlet)												
Open	11a	10a	12a	12a	15a	13a	10a	11a	23b	22a	21a	21a
Closed	19a	19a	18a	17a	16a	16a	24a	36b	20a	34a	37a	33a
Onychiurus aramatus Tullberg												
Open	13a	15a	14a	14a	20b	13a	29a	31a	39b	36a	49b	32a
Closed	21a	20a	21a	17a	17a	16a	33a	29a	35a	29a	34a	31a
Bourtiella hortennis (Fitch)												
Open	4a	5a	4a	4a	3a	21b	7a	5a	2b	5a	6a	6a
Closed	2a	3a	3a	3a	26b	3a	6a	29b	6a	10a	83b	12a
ACARI												
Gustavia microcephala (Nicolete)												
Closed	9a	10a	9a	10a	72b	51b	10a	8a	6a	10a	5b	4b
Peloribates europaeus Willman												
Open	10a	11a	10a	15a	12a	13a	14a	15a	32b	18a	9b	12b
Closed	54a	49a	50a	49a	179b	40a	59a	162b	62a	63a	41b	39b
Peloribates sp. A												
Closed	1a	2a	2a	1a	1a	34b	1a	1a	30b	2a	25b	54c
Peloribates sp. B												
Closed	38a	43a	41a	42a	17b	63c	39a	19b	72c	40a	19b	21b
Ophidiotrichus sp.												
Open	29a	27a	27a	32a	14b	18b	30a	21b	15b	34a	10b	2c
Zygoribatula sp. A												
Open	49a	41a	57a	54a	78b	59a	74a	82a	81a	89a	193b	99a
Closed	90a	81a	83a	101a	115a	153b	111a	109a	149b	143a	162a	210b
Zygoribatula sp. B												
Open	4a	5a	5a	7a	9a	8a	11a	15b	16a	10a	19b	24b
Closed	8a	7a	8a	10a	18b	11a	19a	12b	31c	24a	33b	31b
Zygoribatula sp. C												
Closed	8a	8a	6a	9a	0b	15c	11a	0b	24c	10a	0b	38c
Ledermuelleria pectinata (Ewing)												
Closed	0a	0a	0a	0a	15b	0a	0a	29b	0a	0a	38b	0a
Xenillus sp.												
Closed	15a	14a	14a	30a	0b	45c	39a	0b	96c	41a	0b	108c
THYSANURA												
Lepismatidae												
Open	2a	1a	2a	3a	3a	1b	3a	3a	1b	4a	3a	1b
Closed	4a	3a	3a	4a	3a	2b	5a	6a	1b	7a	8a	4b

[a]Means within a posttreatment time for a species followed by different letters differ significantly ($P < .05$).

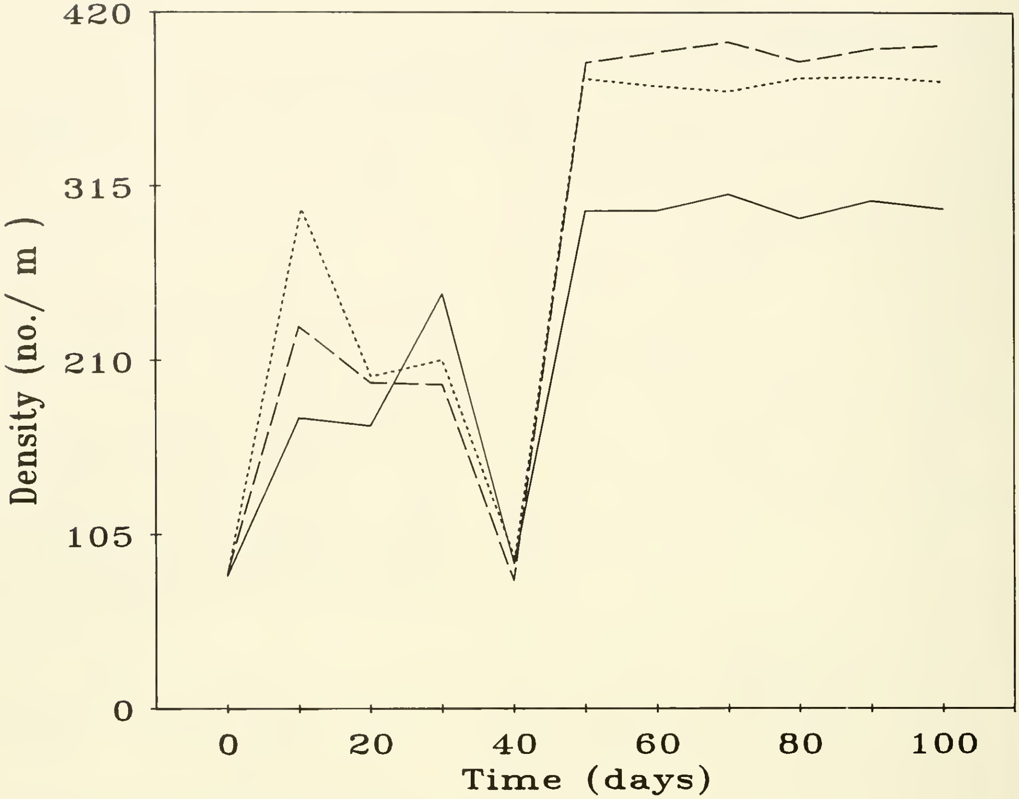

Fig. 1. Density of litter and soil mites in open areas in mountain brush habitats that were untreated (____), mowed (- - - -), or herbicide treated (— — —).

decrease in litter decomposition following application of carbaryl in a grassland habitat; the effects on arthropod abundance lasted only a few days following a single insecticide treatment. These treatments, which adversely affect arthropod populations, may be expected to result in alterations of nutrient availability and cycling (Christiansen 1989); the effects of such treatments will likely be delayed or long-term in nature but should be seriously considered in any shrub management program.

Insecticide applications in mowed plots decreased ($P > .10$) litter decomposition under sagebrush but significantly increased ($P < .05$) decomposition in open, grassy areas. Conversely, herbicide-treated plots showed a significant decrease ($P < .05$) in litter decomposition in open plots and an increase ($P > .10$) in decomposition in closed areas following insecticide applications. The anomolous, significant increase in litter decomposition in open microhabitats of insecticide-treated, mowed plots could have been the result of two interacting factors. The litter accumulated in open areas may have reduced the penetration of insecticides, and the availability of sulfur and phosphorous from the degradation of carbaryl and malathion may have accelerated decomposition (Melnikov 1971). These elements are a main source of energy for fungal and bacterial litter decomposers, and these organisms may have been of primary importance in the increased decomposition rate.

Decreases in the abundance of litter arthropods caused by insecticide applications generally lead to significant decreases in litter decomposition. In some instances, insecticides may indirectly facilitate litter decomposition by providing essential nutrients to fungal and bacterial decomposers. Given the significant effects of insecticide applications on the decomposition of litter by arthropods, the widespread use of these compounds in controlling rangeland insects should be

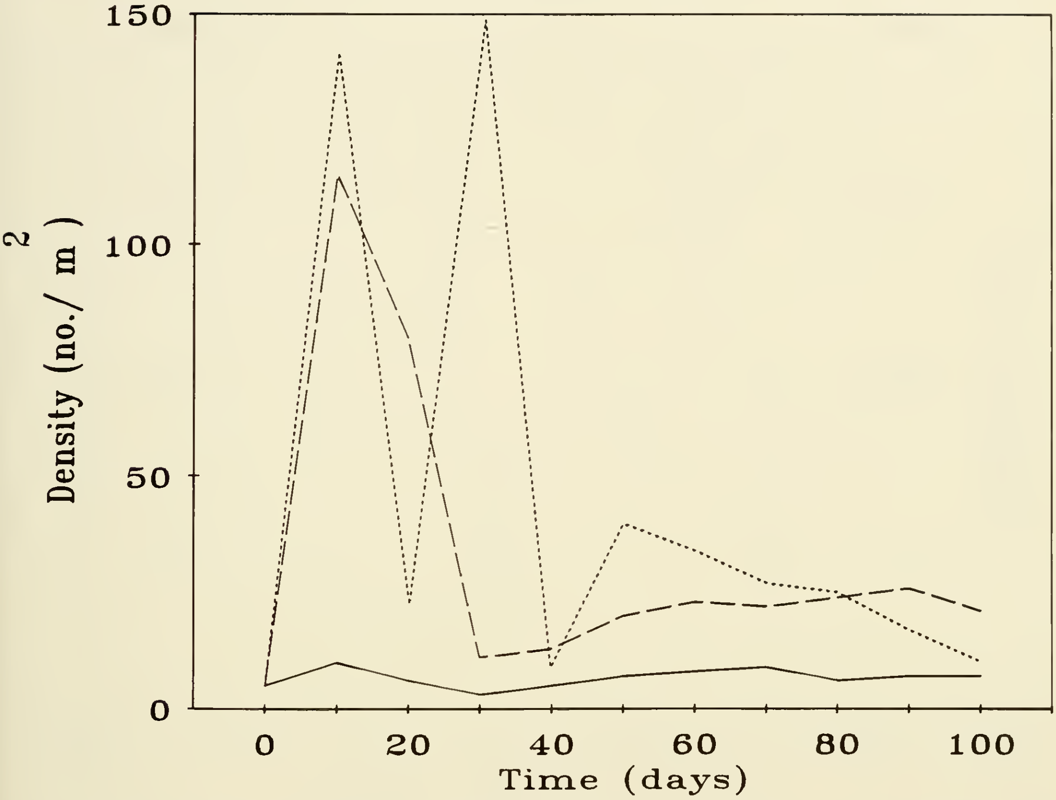

Fig. 2. Density of litter and soil collembolans in open areas in mountain brush habitats that were untreated (____), mowed (- - - -), or herbicide treated (— — —).

TABLE 5. Effects of insecticide treatments on litter arthropod detritivore population densities (no./m^2) in unmanaged, mowed, and herbicide-treated blocks.

	Unmanaged[a]		Mowed		Herbicide	
	con	trt	con	trt	con	trt
Acari	395	87	595	148	643	154
Collembola	42	9	98	25	33	8
Thysanura	4	0	5	0	3	0
% decrease	78		76		76	

[a] con = untreated control; trt = treated with insecticides.

reevaluated. Although many pest insects are frequently not abundant in mountain shrub habitats (e.g., rangeland grasshoppers) and rangeland pests are not treated as intensively as in our study, the inclusion of these habitats in large-scale treatments is a matter of concern. The long-term impact of reducing litter arthropod populations is not known at this time, but it is reasonable to assume that nutrient cycles within the habitat will be disrupted.

ACKNOWLEDGMENT

We thank C. C. Burkhardt for assistance with pesticide applications and P. Lew for field and laboratory assistance. This project was partially funded by USDA-CSRS Grant 85-CSRS-2-2702.

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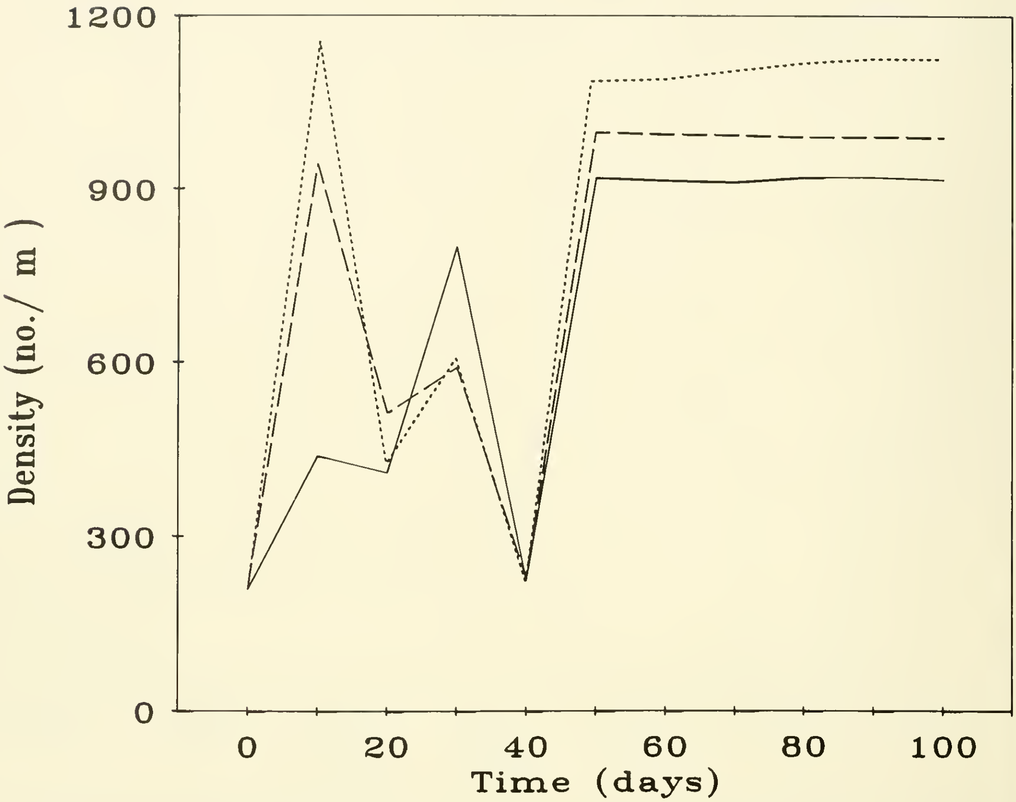

Fig. 3. Density of litter and soil mites in closed areas in mountain brush habitats that were untreated (____), mowed (- - - -), or herbicide treated (— — —).

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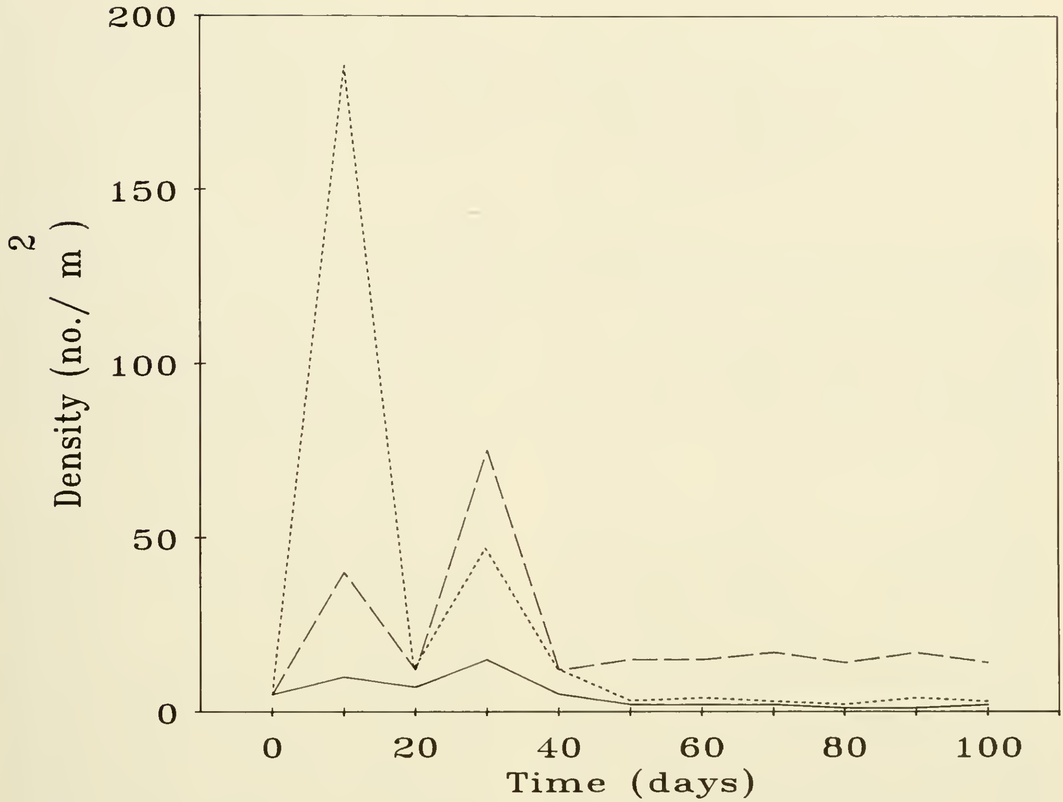

Fig. 4. Density of litter and soil collembolans in closed areas in mountain brush habitats that were untreated (____), mowed (- - - -), or herbicide treated (— — —).

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ARTHROPOD COMMUNITY DYNAMICS IN UNDISTURBED AND INTENSIVELY MANAGED MOUNTAIN BRUSH HABITATS

Tim A. Christiansen[1], Jeffrey A. Lockwood[1], and Jeff Powell[2]

ABSTRACT.—The population dynamics of litter and foliage arthropods in undisturbed and intensively managed sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*) habitats in southeastern Wyoming were assessed by the measurement of density and the determination of indices of diversity, richness, and evenness. Brush management consisted of either mowing to a 20-cm stubble or applying the herbicide 2,4-D butyl ester. A total of 63 arthropod species were found in foliage and 150 species in litter. Mowing and herbicide applications resulted in significant changes in the density of 16 of the 46 major arthropod foliage species and 56 of the 70 major litter species. Diversity increased, except in Hymenoptera and Coleoptera, in both mowed and herbicide-treated foliage. In foliage, richness generally increased in all orders following mowing, and evenness tracked diversity. In litter, the diversity of Coleoptera decreased following mowing and herbicide application in Collembola, Homoptera, and Diptera. Evenness followed diversity in trends in both treatments. Soil arthropods were absent in this habitat before and after treatments.

Although extensive studies of arthropod ecology have been conducted in western grasslands (Blocker et al. 1971, McDaniel 1971, and Kumar et al. 1976), virtually nothing is known concerning the role of arthropods in mountain brush habitats. Sagebrush (*Artemisia* spp.)-dominated grasslands of the western United States cover more than 100 million ha (Beetle 1960). Sagebrush is considerably less palatable to livestock than other range plants such as annual grasses. For this reason, burning, herbicide applications, and mowing are commonly used to rid an area of undesirable range plants and have been used in attempts to eradicate sagebrush (Wright et al. 1979, Powell 1970).

In addition to direct eradication efforts, approximately 10% of the sagebrush habitat in the western United States has been cleared for cultivation and forage production since the early 1900s (Beetle 1960).

Rangeland management practices may have significant effects on the arthropod communities in grassland habitats (Morris 1973, Lloyd and Kumar 1977). While it is clear that such disturbances in sagebrush communities enable economically more desirable annuals to populate range areas, nothing is known regarding the impact on arthropod populations. Habitat disturbance can influence arthropod densities, species distribution, and community diversity. During disturbance and succession, changes in plant diversity and resource availability affect insect diversities (Murdoch et al. 1972, Southwood et al. 1979). Following a disturbance, early successional stages usually include plants with greater palatability than in either the original habitat or later successional stages (Cates and Orians 1975). The amount and type of litter is also affected by abiotic and biotic factors that may be drastically altered by rangeland management practices. A number of factors influence arthropod response to habitat disturbance, including dispersal, host selection, resource availability, litter composition, and vegetation recovery (Schowalter 1985). The objectives of this study were to determine the normal arthropod taxa and population dynamics and to ascertain the immediate impacts of mowing and herbicide application on arthropod communities in a mountain brush habitat. To this end, arthropod populations were monitored in the baseline (1985), treatment (1986), and recovery (1987) years in sites that were either undisturbed or intensively managed.

MATERIALS AND METHODS

This study was conducted on a sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*) habitat, located at an elevation of 2,400 m, 12 km southeast of Saratoga, Carbon County, Wyoming. The soil is North

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Park Formation of brown, sandy loams developed of loess, limestone, sandstone, and tuff. The average yearly precipitation is 48 cm, with most of the moisture being provided by snow. The mean annual temperature is 10.2 C, with a range of 21.0 to 27.0 C during the sampling period of this study.

Habitat manipulation consisted of either mowing to a 20-cm stubble height or applying 2,4-D butyl ester in water at a rate of 0.91 kg per acre in June of 1986. Within each treatment and control, four blocks of at least 8 ha were randomly chosen from sites with similar vegetation and soil characteristics.

Arthropod samples from foliage, litter, and soil in the control and treatment blocks were collected every 10 days from the end of May through mid-September in 1985, 1986, and 1987. Samples were taken along three 100-m transects in each block. The location of the first transect in each block was randomly determined, and the other two transects were placed 70 m from and parallel to the first transect. The sequence of sampling each block was also randomly determined in every sampling period in order to eliminate any chance of systematic errors as a consequence of block location and time of day.

Five samples of foliage arthropods were collected from both closed (canopy/shrub-covered) and open (grass-covered) areas along each transect. Arthropods were collected by enclosing foliage in a 114 l plastic container into which carbon dioxide was released for several minutes. A D-vac was then used to collect the specimens, which were subsequently stored at −5 C.

Litter arthropods were collected on the same days as foliage arthropods. Five open areas and five closed areas were sampled along the same transects as were used for foliage samples. Sampling consisted of collecting all loose litter in a 0.5-m^2 quadrant. The arthropods were separated from the litter in the laboratory by use of Berlese funnels and then stored in 70% ethanol.

Soil cores for each treatment and block were taken along the same transects as foliage and litter collections. These cores were taken several days before foliage and litter collections so that the arthropods would not be disturbed for foliage collection. A core 10 cm deep and 5 cm in diameter was taken every 10 m along each transect. Five samples were taken from both open and closed areas. Separation of arthropods from the soil was accomplished by flotation in a 20% dilute magnesium sulfate solution (Salt and Hollick 1944) or a heptane solution (Walter et al. 1987). Also, each sample was subdivided and examined under a dissecting microscope at 20X to detect soil arthropods.

Samples were pooled between seasons and blocks to provide estimates of ecological indices and the density of each major species (i.e., those that accounted for at least 5% of an order) in foliage, litter, or soil in each treatment and control site. The densities across treatments were compared using the protected least significant difference post-ANOVA test. Differences were considered significant at $P < .05$. Diversity was expressed using the natural logarithm form of the Shannon-Weaver index; evenness was calculated using Pielou's J, and richness was expressed as the number of species present (Poole 1974).

RESULTS

The brush management procedures resulted in significant decreases in the total shrub cover. Herbicide application reduced shrub cover to 59% and 57% of the baseline level (which was 30% of the total area before treatment) in the treatment and recovery years, respectively. Mowing reduced shrub cover to 75% and 72% of the baseline level (which was 32% of the total area before treatment) in the treatment and recovery years, respectively. Sagebrush was generally reduced to a greater extent than bitterbrush.

A total of 150 arthropod species were collected in litter, of which 70 were considered major species (Table 1). Mowing and herbicide applications resulted in significant changes in the density of 57 of these 70 species in the treatment year. Following mowing, 17 species significantly decreased and 22 species significantly increased in density. After herbicide treatment, 16 species significantly decreased and 27 species significantly increased in density. All orders included species that were significantly impacted by management.

A total of 63 arthropod species were found in foliage, of which 46 were considered major species (Table 2). Mowing and herbicide application resulted in significant changes in the density of 16 of these 46 species during the

TABLE 1. Effects of sagebrush/bitterbrush control on litter arthropods.

				Density (no./m^2)[a]		
Order/Family	Genus	Species	Year	Control	Mowed	Herbicide
COLLEMBOLA						
Entomobryidae	*Orehesella*	*hexafasciata* Harvey	1985	6aA	4aA	4aA
			1986	1aA	11bB	4abA
			1987	11aB	22bC	21bB
Isotomidae	*Isotoma*	*tennis* Folsom	1985	1aA	3aA	1aA
			1986	5aB	2bA	1bA
			1987	0aA	5abA	8bB
	Isotoma	sp.	1985	6aA	5aA	7aA
			1986	2aA	10bB	36cB
			1987	17aB	7bA	18aC
Onychiuridae	*Onychiurus*	sp. A	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	2aA	4aB	5aB
	Onychiurus	sp. B	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	2aA	25bB	2aA
Sminthuridae	*Bourtella*	*hortennis* (Fitch)	1985	3aA	5aA	3aA
			1986	6aA	70bB	36cB
			1987	0aA	0aA	1aA
PSCOPTERA						
Liposcelidae	*Liposcelis*	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	16aB	7bB	20aB
Psocidae	*Psocidus*	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	13aB	48bB	13aB
Psyllipsocidae	*Psocatropes*	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	44aB	61aB	52aB
THYSANURA						
Lepismatidae	unknown		1985	5aA	5aA	6aA
			1986	6aA	5aA	3bA
			1987	3aA	5aA	14bB
	unknown		1985	3aAB	4aA	1aA
			1986	0aA	3bA	0aA
			1987	5aB	14bB	9abB
Nicoletiidae	unknown		1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	2aA	1aA	5bB
HEMIPTERA						
Miridae	*Lygus*	*robustus* (Uhler)	1985	1aA	3aA	2aA
			1986	0aA	0aA	0aA
			1987	5aB	0bA	2abA
	Slaterocoris	*robustus* (Uhler)	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	4aB	10bB	4aB
HOMOPTERA						
Aphidae	*Macrosiphum*	*californicum* (Clarke)	1985	0aA	3aA	2aA
			1986	0aA	0aA	1aA
			1987	0aA	5bA	5bB
	Macrosiphum	sp.	1985	4aA	3aA	3aA
			1986	5aA	0bA	1bA
			1987	17aB	17aB	16aB

TABLE 1 continued.

	Brachycaudus	*cardui* (L.)	1985	4aA	3aA	3aA
			1986	5aA	0bA	1bA
			1987	3abA	0aA	7bB
	Myzus	sp.	1985	1aA	1aA	0aA
			1986	0aA	2bA	0aA
			1987	1aA	0aA	3aA
Cicadellidae	*Idiocerus*	*ensiger* Ball	1985	1aA	1aA	1aA
			1986	1aA	5bB	2aA
			1987	0aA	0aA	5bB
	Macrosteles	*fascifrons* (Stahl)	1985	2aA	1aA	1aAB
			1986	3aA	1abA	0bA
			1987	1abA	0aA	3bB
	Empoasca	sp.	1985	0aA	0aA	1aA
			1986	0aA	taA	1abA
			1987	0aA	1aA	1aA
Delphacidae	*Laccocera*	*flava* (Crew.)	1985	1aA	1aA	1A
			1986	1aA	1aA	4bB
			1987	0aA	0aA	0aA
COLEOPTERA						
Carabidae	*Carabus*	*taeclatus oregonensis* LeC.	1985	1aA	2aA	1aA
			1986	taA	1aA	1aA
			1987	2aA	2aA	1aA
	Harpalus	*fraternus* LeC.	1985	0aA	0aA	0aA
			1986	0aA	1aA	0Aa
			1987	1aA	1aA	0aA
	Cymindis	*planipennis* LeC.	1985	1aA	1aA	0aA
			1986	1aA	taA	0aA
			1987	1aA	1aA	0aA
Curculionidae	*Sitona*	*lineata* L.	1985	1aA	1aA	2aA
			1986	1aA	3aA	3aA
			1987	2aA	3aA	9bB
	Diamimus	*gubsericeus* Horn	1985	1aA	1aA	1aA
			1986	2aA	2aA	2aA
			1987	2aA	1aA	1aA
Staphylinus	*Oxytelus*	sp.	1985	2aA	0aA	0aA
			1986	3aA	0bA	0bA
			1987	1aA	0aA	0aA
	Stenus	sp.	1985	1aA	1aA	1aA
			1986	1aA	1aA	4bB
			1987	1aA	1aA	3bAB
	Staphylinus	*maxillosus* Gravenhorst	1985	0aA	0aA	0aA
			1986	0aA	1aA	0aA
			1987	1aA	1aA	0aA
Coccinellidae	*Hippodamia*	*convergens* Guerin	1985	2aA	0aA	0aA
			1986	3aA	0bA	0bA
			1987	3aA	0bA	0bA
Tenebrionidae	*Asidopsis*	*polita* (Say)	1985	1aA	1aA	2aA
			1986	1aA	0aA	0aA
			1987	0aA	5bB	0aA
Meloidae	*Meloe*	*angustico* Say	1985	1aA	1aA	1aA
			1986	1aA	0aA	0aA
			1987	1aA	0aA	0aA
DIPTERA						
Ceratopognidae	*Culicoides*	sp.	1985	2aA	1aA	1aA
			1986	2aA	taA	taA
			1987	7aB	10aB	3bA

TABLE 1 continued.

Phoridae	*Megaselia*	sp.	1985	1aA	1aA	2aA
			1986	taA	1aA	2aA
			1987	6aB	10aB	6aB
Chironomidae	*Chironomus*	sp.	1985	0aA	1aA	1aA
			1986	0aA	3bA	10cB
			1987	1aA	1aA	0aA
Sarcophagidae	*Sarcophaga*	*haemorrhoidalis* (Fallen)	1985	6aA	5aAB	6aA
			1986	6abA	7aB	4bA
			1987	4aA	3aA	4aA
	Taxigramma	*heteroneura* (Meigen)	1985	2aA	0aA	0aA
			1986	3aA	0bA	0bA
			1987	2aA	0aA	0aA
Simuliidae	*Simuliumxum*	*nigricoxum* Stone	1985	1aA	1aA	1aA
			1986	0aA	2aA	1aA
			1987	0aA	1aA	1aA
Otitadae	unknown		1985	10aA	11aA	10aA
			1986	13aA	0bB	1bB
			1987	1aB	7bC	6bC
Scatophagidae	*Scatophaga*	*stercoraria* (L.)	1985	1aA	0aA	0aA
			1986	0aA	0aA	3bB
			1987	0aA	0aA	3bB
Empididae	*Platypalpus*	*sutor* Rjelander	1985	1aA	0aA	0aA
			1986	0aA	0aA	5bB
			1987	0aA	1abA	3bB
HYMENOPTERA						
Formicidae	*Amblypone*	sp.	1985	1aA	0aA	1aA
			1986	1aA	taA	1aA
			1987	3aB	1bA	1bA
	Camponotus	*astus* Forel	1985	4aA	3aA	3aA
			1986	5aA	2bA	4abA
			1987	3aA	1aA	9bB
	Cyphomynmex	*rimosus* (Spinola)	1985	1aA	1aA	1aA
			1986	1abA	2bA	0aA
			1987	1abA	2bA	0aA
	Monomorium	*carbonarium* (L.)	1985	4aA	4aA	3aA
			1986	4aA	5aA	8bB
			1987	3aA	6bA	0cC
	Paratrechina	*vividula* (Nylander)	1985	2aAB	2aA	1aA
			1986	3aA	2abA	tbA
			1987	0aB	0aA	0aA
	Ponera	*trigona* Mayr.	1985	1aA	1aA	1aA
			1986	1aA	taA	0aA
			1987	0aA	0aA	0aA
	Solenopsis	sp.	1985	1aA	1aA	0aA
			1986	1aA	1aA	0aA
			1987	0aA	0aA	0aA
ACARI						
Haplozetidae	*Peloribates*	*europacus* William	1985	12aA	10aA	10aA
			1986	69aB	63aB	45bB
			1987	0aC	0aC	3bC
	Peloribates	sp. A	1985	1aA	1aA	0aA
			1986	1aA	28bB	8cB
			1987	5aB	31bB	57bC
	Peloribates	sp. B	1985	30aA	28aA	28aA
			1986	41aA	16bA	63cB
			1987	22aA	1bB	2bC

Table 1 continued.

Orbatulidae	*Zygoribatula*	sp. A	1985	101aA	98aA	110aA
			1986	139aA	213aB	166aA
			1987	93aA	51aA	90aA
	Zygoribatula	sp. B	1985	20aA	21aA	20aA
			1986	12aA	25bA	30bA
			1987	58aB	25bA	26bA
	Zygoribatula	sp. C	1985	10aA	11aA	11aA
			1986	8aA	0bB	33cB
			1987	26aB	96aC	3bC
	Zygoribatula	sp. D	1985	174aA	183aAB	179aA
			1986	181aA	153aA	178aA
			1987	265aB	212aB	262aB
Gustaviidae	*Gustavia*	*microcephala* (Nicoleie)	1985	12aA	18aA	11aA
			1986	10aA	124bB	50cB
			1987	77aB	130bB	26cC
Xenillidae	*Xenillus*	sp.	1985	25aA	20aA	24aA
			1986	30aA	0bB	95cB
			1987	0aB	0aB	0aC
Macrochelidae	*Petridiobus*	sp.	1985	4aA	4aA	3aAB
			1986	6aA	2bAB	6aA
			1987	0aB	0aB	0aB
Oribatellidae	*Ophidiotrichus*	sp. A	1985	21aA	24aA	21aA
			1986	38aA	0bB	1bB
			1987	67aB	61aC	63aC
	Ophidiotrichus	sp. B	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	3aB	5aB	5aB
Stigmaeidae	*Ledermuelleria*	*pectinata* (Ewing)	1985	0aA	1aA	1aA
			1986	0aA	26bB	0aA
			1987	21abB	12bC	33aB
	Ledermuelleria	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	0aA	4bB	4bB
Araneae						
Lycosidae	*Lycosa*	*punctulata*	1985	1aA	1aA	1aA
			1986	1aA	2aA	2aA
			1987	3aA	2aA	2aA
	Lycosa	sp.	1985	0aA	0aA	0aA
			1986	1aA	0aA	0aA
			1987	5aB	4aB	9bB
Salticidae	*Metaphidippus*	*insignis* (Banks)	1985	1aA	1aAB	2aA
			1986	0aA	0aA	2aA
			1987	2aA	3aB	0aA
	Pellenes	sp.	1985	0aA	0aA	0aA
			1986	0aA	3bB	0aA
			1987	0aA	0aA	0aA
Tetranathidae	*Leucauge*	*venusta* (Walckenaer)	1985	0aA	1aA	1aA
			1986	0aA	0aA	1aA
			1987	5aB	4aB	0bA
Thomisidae	*Misumenoides*	*formosipes* (Walckenaer)	1985	4aA	3aA	3aAB
			1986	6aA	3abA	1bA
			1987	0aB	2abA	5bB
	Misumenoides	*vatia* (Hentz)	1985	1aA	0aA	1aA
			1986	0aA	0aA	1aA
			1987	0aA	0aA	0aA

TABLE 1 continued.

	Misumenoides	sp.	1985	0aA	1aA	1aA
			1986	0aA	0aA	2aA
			1987	0aA	0aA	1aA
	Misumenoides	*asperatus* (Hentz)	1985	1aA	1aA	1aA
			1986	2aA	0bA	0bA
			1987	2aA	0bA	0bA
Thomisidae	*Oxyptila*	sp.	1985	1aA	1aA	1aA
			1986	1aA	0aA	0aA
			1987	3aA	2aA	6bB

[a]Means for a species within a year followed by different lower-case letters differ significantly at the P ≤ .05 level. Means for a species within a treatment regime followed by different upper-case letters differ significantly at the P ≤ .05 level, t = a trace density less than one but greater than zero.

treatment year. Following mowing, three species significantly decreased in density and six species significantly increased in density. After herbicide treatment, six species significantly decreased in density and two species significantly increased in density.

Collembola included six major litter species. Two species appeared and one species disappeared in the year following treatments (Table 1). Mowing of habitats significantly increased density of three species and significantly decreased density of one species. In the recovery year, two species continued to increase significantly in density and two species decreased significantly. Herbicide application initially had the effect of significantly increasing the density of two species. The initial increase of these two species did not continue the following year; densities were lower than those found in unmanaged sites. The three species that did not change significantly during the treatment year increased in density during the recovery year. Of the two species appearing in the recovery year, one increased significantly in mowed sites. Only one individual was collected on foliage (Table 2).

Psocoptera litter species did not appear in unmanaged or disturbed sites until the recovery year (Table 1). Of the three major species, the density of one was significantly lower in mowed sites than in unmanaged sites, and the density of another species was significantly greater in mowed sites than in either undisturbed sites or herbicide-treated sites. In the recovery year, the density of foliage Psocoptera in mowed and herbicide-treated sites was significantly lower than in undisturbed sites (Table 2).

Thysanura species found in litter were not significantly affected until the recovery year, at which time the density of two species increased significantly in herbicide-treated sites and one species increased significantly in density in mowed sites (Table 1).

Two species of Thysanoptera appeared in foliage during the recovery year (Table 2).

Hemiptera were not abundant in litter. One species disappeared in the treatment year, and another species appeared in the recovery year (Table 1). Hemipteran populations comprised only 3% of the foliage arthropod density. Members of this order did not appear in the study site until the recovery year. Herbicide-treated sites had significantly lower densities of all three species than unmanaged sites. Mowed sites harbored two species that had significantly lower densities than in unmanaged habitats (Table 2).

Homoptera was one of the richest orders in the litter component. Three aphid species significantly increased in density in mowed or herbicide-treated sites (Table 1). Several aphid species had density increases of over 100% in the recovery year in herbicide-treated sites, and the density of one species increased significantly in mowed sites. Generally, disturbance had little effect on litter population densities of the Cicadellidae. Delphacidae had one species with sufficient density to be included in the analysis. The density of this species increased significantly during the year in which herbicide was applied. Homoptera constituted 30% of all species found in the foliage component of this sagebrush/bitterbrush system. All of the five major species of aphids were significantly affected by mowing or herbicide application. Mowing and herbicide application significantly decreased density in the treatment year in two species, while mowing significantly increased the density of one species during the treatment year. In three of the five species, density

TABLE 2. Effects of sagebrush/bitterbrush control on foliage arthropods.

				Density (no./m^2)[a]		
Order/Family	Genus	Species	Year	Control	Mowed	Herbicide
COLLEMBOLA						
Sminthuridae	*Bourtella*	*hortennis* (Fitch)	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	taA	0aA	0aA
PSOCOPTERA						
Psocidae	*Psocidae*	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	27aB	4bB	0cA
THYSANOPTERA						
Aeolothripidae	*Stomatothrips*	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	14aB	12aB	14aB
Thripidae	*Frankliniella*	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	1aA	0aA	0aA
HEMIPTERA						
Miridae	*Lygus*	*robustus* (Uhler)	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	26aB	21aB	6bB
	Lygus	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	12aB	4bB	3bB
	Slaterocoris	*robustus* (Uhler)	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	22aB	7bB	4bB
HOMOPTERA						
Aphidae	*Brachycaudus*	*cardui* (L.)	1985	29aA	32aA	27aA
			1986	43aA	11abB	3bB
			1987	79aB	51abA	36bA
	Cinera	*pseudotsugae* (Walker)	1985	98aA	103aA	100aA
			1986	109aA	2bB	0bB
			1987	290aB	0bB	45cC
	Myzus	*solani* (Sulzer)	1985	0aA	0aA	0aA
			1986	0aA	1aA	2aA
			1987	0aA	0aA	0aA
	Myzus	sp.	1985	0aA	0aA	0aA
			1986	0aA	10bB	0aA
			1987	0aA	7bB	4abB
	Macrosiphium	sp.	1985	1aA	2aAB	2aA
			1986	2aA	3aA	1aA
			1987	2aA	0aB	0aA
Cicadellidae	*Parabolocrates*	*major* Osb.	1985	20aA	19aA	21aA
			1986	32aA	3bB	6bB
			1987	0aB	18bA	17bA
	Idiocerus	*ensiger* Ball	1985	2aAB	1aA	2aAB
			1986	3aA	0bA	3aA
			1987	0aB	0aA	0aB
	Cuerna	*striata* (Walker)	1985	0aA	0aA	0aA
			1986	0aA	0aA	2aA
			1987	0aA	0aA	0aA
Membracidae	*Pubilia*	*modesta* Uhler	1985	10aA	12aA	12aA
			1986	14aA	0bB	6cB
			1987	0aB	0aB	0aC

TABLE 2 continued.

Delphacidae	*Laccocera*	*obesa* VanDuzee	1985	0aA	0aA	0aA
			1986	0aA	1aA	5bB
			1987	0aA	0aA	0aA
	Laccocera	*flava* (Crew.)	1985	3aA	4aA	4aA
			1986	4aA	1aAB	2aAB
			1987	6aA	0bB	0bB
Psyllidae	*Psylla*	*galeaformis* Patch.	1985	1aA	1aA	2aA
			1986	1aA	0aA	3aA
			1987	0aA	1aA	1aA
	Psylla	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	0aA	4bB	3abA
COLEOPTERA						
Staphylinidae	*Stenus*	sp.	1985	1aA	1aA	1aA
			1986	1aA	6bB	2aA
			1987	1aA	2aA	0aA
	Staphylinus	*maxillosus*	1985	0aA	0aA	0aA
			1986	0aA	taA	1aA
			1987	0aA	0aA	0aA
Scarabaeidae	*Canthon*	*praticola* LeC.	1985	0aA	0aA	0aA
			1986	0aA	taA	taA
			1987	0aA	0aA	0aA
Curculionidae	*Sitona*	*lineata* L.	1985	0aA	0aA	0aA
			1986	1aA	3aB	2aA
			1987	1aA	0aA	0aA
Carabidae	*Pterostichuis*	*proctractus* LeC.	1985	0aA	0aA	0aA
			1986	1aA	0aA	0aA
			1987	0aA	0aA	0aA
	Carabus	*taeclatus oregonensis* LeC.	1985	0aA	0aA	0aA
			1986	0aA	0aA	1aA
			1987	0aA	0aA	0aA
Coccinellidae	*Hippodamia*	*convergenes*	1985	3aA	2aA	3aA
			1986	3abA	6aB	0bB
			1987	0aB	0aA	0aB
DIPTERA						
Bibionidae	*Bibio*	*albipennis* Say	1985	0aA	0aA	0aA
			1986	0aA	taA	1aA
			1987	0aA	2aA	0aA
Ceratopogonidae	*Culicoides*	sp.	1985	3aA	4aA	3aA
			1986	5aA	taA	1aA
			1987	13aB	1bA	5bA
Dolichopodidae	*Chrysotus*	*picticopris* Loew	1985	0aA	0aA	0aA
			1986	0aA	3bB	0aA
			1987	0aA	2aAB	2aA
Empididae	*Platypalpus*	*sutor* Rjelander	1985	6aA	5aA	5aA
			1986	8aA	tbB	0bB
			1987	1aB	0aB	0aB
Otitidae	*Melieria*	*occidentalis* Coq.	1985	1aA	0aB	0aA
			1986	0aA	0aA	0aA
			1987	129aB	109aB	30bB
Phoridae	Unknown		1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	34aB	58aB	85bB
HYMENOPTERA						
Braconidae	*Macrocentrus*	sp.	1985	3aA	2aA	3aA
			1986	3aA	2aA	1aA
			1987	47aB	45aB	18bB

TABLE 2 continued.

Formicidae	*Ambypone*	sp.	1985	1aA	2aA	1aA
			1986	taA	taA	6aB
			1987	0aA	0aA	0aA
	Cyphomyrmex	*rimous*	1985	20aA	19aA	24aA
			1986	23aA	38bB	23aA
			1987	47aB	18bA	45aB
	Monomorium	*carbonarium*	1985	0aA	0aA	0aA
			1986	0aA	1aA	5bB
			1987	0aA	0aA	0aA
	Paratrechina	*vividula*	1985	6aA	5aA	5aA
			1986	6aA	7aA	6aA
			1987	9aA	17aB	16aB
	Pogonomyrmex	*barbatus* (Smith)	1985	1aA	3aA	1aA
			1986	2abA	1aA	10bB
			1987	17aB	8bB	0cA
	Pogonomyrmex	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	129aB	0bA	0bA
	Ponera	*trigona* (Forel)	1985	2aA	3aA	3aA
			1986	3aA	11aB	15aB
			1987	13aB	70bC	16aB
	Ponera	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	4bB	0aA	0aA
	Solenopsis	*germinata* (F.)	1985	7aA	7aA	6aA
			1986	7aA	12aA	16aB
			1987	0aB	0aB	0aC
	Solenopsis	*azteca pallida* Wheeler	1985	5aA	7aA	6aA
			1986	14aB	tbB	0bB
			1987	0aC	3bB	2abB
	Solenopsis	sp.	1985	0aA	0aA	0aA
			1986	0aA	0aA	0aA
			1987	11aB	14aB	2bA
	Strumigenys	*eggersi* Emery	1985	4aA	7aA	3aA
			1986	6aA	1aB	3aA
			1987	0aB	0aB	0aB
ACARI						
Orbitellidae	*Orphidiotrichus* sp.		1985	0aA	0aA	0aA
			1986	0aA	2aA	0aA
			1987	0aA	0aA	0aA
Macrochelidae	*Macrocheles*	*musedomesticae* (Scopol.)	1985	0aA	0aA	0aA
			1986	0aA	0aA	1aA
			1987	0aA	0aA	0aA
Orbatulidae	*Zygoribatula*	sp.	1985	1aA	0aA	0aA
			1986	taA	0aA	1aA
			1987	0aA	0aA	0aA
ARANEAE						
Araneidae	*Araniella*	*displicata* (Hentz)	1985	3aA	0bA	0bA
			1986	4aA	0bA	0bA
			1987	0aB	0aA	0aA
Lycosidae	*Lycosa*	*punctulata* Hentz	1985	1aAB	1aA	0aA
			1986	0aA	1aA	0aA
			1987	3aB	2aA	1aA
	Lycosa	*gulosa* (Walckenaer)	1985	1aA	1aA	1aA
			1986	0aA	taA	1aA
			1987	10aB	14aB	4bB

TABLE 2 continued.

Oxyopidae	*Oxyopes*	sp.	1985	1aA	0aA	2aA
			1986	0aA	taA	taA
			1987	5aB	4aB	2aA
Salticidae	*Metaphidippus*	*insignis*	1985	0aA	0aA	0aA
			1986	0aA	1aA	0aA
			1987	0aA	8aB	1aA
Thomisidae	*Misumena*	*vatia* (Clerck)	1985	0aA	0aA	0aA
			1986	taA	1aA	1aA
			1987	0aA	0aA	1aA
	Misumenoides	*formosipes* (Walckenaer)	1985	0aA	0aA	0aA
			1986	0aA	taA	taA
			1987	3aB	5aB	0bA
	Misumenops	*asperatus* (Hentz)	1985	0aA	0aA	0aA
			1986	1aA	taA	1aA
			1987	0aA	0aA	2aA
	Oxyptila	sp.	1985	0aA	0aA	0aA
			1986	1aAB	0aA	0aA
			1987	3aB	2aA	3aB

[a] Means for a species within a year followed by different lower-case letters differ significantly at the $P \leq .05$ level. Means for a species within a treatment regime followed by different upper-case letters differ significantly at the $P \leq .05$ level; t a trace density less than one but greater than zero.

returned to pretreatment levels during the recovery year (Table 2).

Coleoptera had 11 major species in the litter component of this sagebrush/bitterbrush system. Carabidae, which comprised 37% of the beetles, were not significantly affected by any disturbance (Table 1). Staphylinids, which comprised 36% of the beetles, had one species increase significantly in herbicide-treated sites during the treatment year. Treatments increased the densities of one-third of the coleopteran species found in foliage. Recovery from treatments to densities found in unmanaged habitats did not occur for any foliage beetle species (Table 2).

Dipteran species comprised 14% of the foliage arthropod fauna. Initially, treatments significantly affected only two of the six major species. However, in the recovery year, densities of five of the six major species significantly increased in mowed or herbicide-treated sites (Table 2).

There were seven major species of ants found in litter, of which four were affected by management practices (Table 1). Two species significantly increased in density and two species significantly decreased. Mowed sites contained one ant species that significantly decreased during the treatment year and one species that significantly increased. Ant densities in unmanaged sites were very labile. Six ant species significantly increased in density and three species significantly decreased in density during the recovery year (Table 1). Hymenoptera species comprised 30% of the foliage fauna. There were 12 major species of ants and one major species of wasp in foliage (Table 2). Mowing significantly increased densities of two ant species during the treatment year; however, the densities of these two species significantly declined in the recovery year. Density of one ant species was significantly lowered in the treatment year and continued to be significantly lower, as compared with unmanaged sites, in the recovery year. Densities during the recovery year showed six species significantly lower than in unmanaged sites, and two species significantly increased in density (Table 1). Herbicide application significantly increased five foliage ant species during the treatment year; four of these species showed significant declines in density the following year. In the recovery year, four ant species showed significant density increases in mowed sites.

Acari comprised the largest proportion (21%) of species found in litter samples (Table 1). Mowing disrupted mite populations by significantly increasing five and significantly decreasing three of the 14 major litter species during the treatment year. The recovery year had seven species significantly increase in density and five species significantly decrease in density in litter of mowed sites, as compared with unmanaged sites. Herbicide application resulted in seven litter species significantly increasing and only one species significantly decreasing during the year of disturbance. The recovery year had eight litter species with significant increases in density and four species with significant decreases in density compared with unmanaged sites.

Aranae included 15% of the litter arthropod species. Herbicide application significantly decreased density in one of the 10 litter species (Table 1). During the recovery year, three spider species significantly increased in density in both mowed and herbicide-treated sites. Foliage spider densities were not significantly affected by mowing until increases occurred in four of the nine major foliage species during the recovery year (Table 2). Herbicide application significantly increased three of the nine major species during the recovery year.

Diversity, richness, and evenness of Collembola in unmanaged sites increased over the three-year study (Table 3). Herbicide application decreased diversity during the treatment year; however, by the recovery year diversity had surpassed the baseline level. Likewise, evenness declined during the first year of disturbance but then increased to the level of unmanaged sites. Mowing increased diversity of springtails during the disturbance year and increased both diversity and evenness during the recovery year.

Psocoptera appeared in litter in the treatment year and diversity decreased markedly in all sites between the treatment and recovery years (Table 3).

Thysanuran diversity, richness, and evenness in unmanaged sites decreased in the treatment year but increased in the recovery year (Table 3). Application of herbicide increased diversity and richness in litter in both the treatment and recovery years. Mowing significantly increased richness in the recovery year.

Hemipteran populations did not have sufficient densities for analysis until the recovery year. Diversity in litter in unmanaged sites was twofold greater than in herbicide-treated sites and over threefold greater than in mowed sites (Table 3).

Diversity of homopteran species in litter was increased with mowing and herbicide application in both the treatment and recovery years, compared with the baseline year (Table 3). Richness was relatively higher than in the unmanaged sites during the years of treatment and recovery. Foliage homopteran diversity was greater in treated sites than in unmanaged sites but returned to pretreatment levels by the recovery year (Table 4). Richness significantly increased during the treatment year in both herbicide-treated and mowed sites and significantly decreased in the recovery year.

Mowing decreased coleopteran diversity in litter for the disturbance year; however, by the recovery year diversity in mowed sites was 100% greater than in unmanaged sites (Table 3). Richness decreased significantly in control and herbicide-treated sites in the recovery year. In foliage, coleopteran diversity decreased markedly in herbicide-treated sites in the recovery year.

Dipteran diversity in litter increased in mowed sites in the year of disturbance but decreased in the other sites. Herbicide-treated sites had an increase in diversity by the recovery year (Table 3). Foliage dipteran diversity was increased nearly fourfold in the year of mowing but by the recovery year had declined to the undisturbed level (Table 4).

Hymenopteran richness, evenness, and diversity in litter decreased in mowed sites in the recovery year (Table 3). Foliage hymenopteran richness increased significantly in both mowed and herbicide-treated sites during the year of disturbance. In the recovery year, richness decreased and diversity increased in mowed and herbicide-treated sites (Table 4).

Diversity and richness of litter Acari declined in all sites in the recovery year (Table 3). The brush management practices had little effect on foliage Acari, relative to changes in unmanaged sites (Table 4).

Litter populations of Aranea were very labile in all sites (Table 3). The diversity of spiders decreased in control and herbicide-treated sites in the treatment year and then increased markedly in the recovery year. The decrease in diversity in the treatment year was associated with an increase in evenness in herbicide-treated sites but a decrease in evenness in unmanaged sites. The foliage Aranea were generally more stabile, although diversity increased in all sites in the recovery year. Richness significantly increased in managed sites in the treatment year.

No arthropods were found in the soil cores below the litter layer in either control or treated plots.

TABLE 3. Diversity, richness, and evenness of arthropod populations in litter and their changes between years due to treatments (N = 360 samples).

Order and Treatment	Diversity			Richness[a]			Evenness		
	1985	1986	1987	1985	1986	1987	1985	1986	1987
COLLEMBOLA									
control	.49	.52	.63	3	5	5	.80	.86	.90
herbicide	.47	.34	.55	5	5	4	.78	.57	.92
mowed	.47	.57	.62	4	8	6	.79	.74	.89
PSOCOPTERA									
control	–	.93	.41	–	3	3	–	.86	.86
herbicide	–	1.01	.45	–	4	3	–	.78	.95
mowed	–	.95	.38	–	4	3	–	.68	.80
THYSANURA									
control	.49	–	.63	3	1	5	.96	–	.90
herbicide	<.01	.29	.71	1	2	6	1.00	.95	.92
mowed	.38	–	.65	5	1*	6	.97	–	.83
HEMIPTERA									
control	–	–	.93	–	–	9	–	–	.98
herbicide	–	–	.46	–	–	3	–	–	.97
mowed	–	–	.28	–	–	2	–	–	.92
HOMOPTERA									
control	.45	.59	.32	5	6	3	.94	.85	.67
herbicide	.45	.61	.62	5	8	5	.93	.88	.89
mowed	.58	.71	.59	5	8	5	.87	.92	.84
COLEOPTERA									
control	.76	.85	.29	6	11*	2	.88	.94	.97
herbicide	.76	.73	.19	6	8*	2	.91	.94	.62
mowed	.75	.56	.60	7	6	4	.85	.92	1.00
DIPTERA									
control	.62	.50	.73	5*	11	6	.77	.83	.94
herbicide	.69	.50	.82	5	8	7	.77	.84	.97
mowed	.63	.72	.71	6	12	6	.76	.86	.91
HYMENOPTERA									
control	.61	.76	.56	5	9*	4	.89	.79	.93
herbicide	.55	.59	.68	7	7	5	.87	.70	.97
mowed	.53	.77	.23	5	5*	2	.91	.85	.76
ACARI									
control	.85	.79	.37	17	20*	4	.70	.76	.62
herbicide	.82	.76	.16	17	17*	2	.72	.80	.54
mowed	.82	.85	.47	15	19*	3	.72	.82	.90
ARANEAE									
control	.54	.37	1.01	5	7	11	.90	.77	.97
herbicide	.53	.30	.68	5	4	5	.89	1.00	.98
mowed	.55	.67	.83	5	7	7	.91	.86	.98

[a] An asterisk indicates that species richness differs significantly ($P < .05$) between adjacent years.

DISCUSSION

Mowed sites generally had increases in arthropod population densities and decreases of richness during the year of disturbance. A study by Bulan and Barrett (1971) showed that mowing increased density and decreased species richness in a grassland habitat. They attributed some of the decrease in richness to the successful competition of a few species in mowed grassland habitats. The decrease in diversity and evenness in our study indicated that a few herbivore arthropod species were dominant during the recovery year. A decrease in species diversity and evenness was

TABLE 4. Diversity, richness, and evenness of arthropod populations in litter and their changes between years due to treatments (N = 360 samples).

	Diversity			Richness[a]			Evenness		
Order and Treatment	1985	1986	1987	1985	1986	1987	1985	1986	1987
COLLEMBOLA									
control	–	–	–	–	–	–	–	–	–
herbicide	–	–	–	–	–	–	–	–	–
mowed	–	–	–	–	–	–	–	–	–
PSOCOPTERA									
control	–	–	–	–	–	1	–	–	–
herbicide	–	–	–	–	–	1	–	–	–
mowed	–	–	–	–	–	1	–	–	–
THYSANOPTERA									
control	–	–	–	–	–	2	–	–	.35
herbicide	–	–	–	–	–	2	–	–	.54
mowed	–	–	–	–	–	1	–	–	–
HEMIPTERA									
control	–	–	.73	–	–	6	–	–	.94
herbicide	–	–	.68	–	–	5	–	–	.97
mowed	–	–	.75	–	–	7	–	–	.89
HOMOPTERA									
control	.36	.58	.32	4	9	4	.80	.65	.53
herbicide	.41	.78	.57	4*	11*	4	.79	.94	.95
mowed	.43	.98	.38	4*	16*	3	.81	.82	.80
COLEOPTERA									
control	.35	.61	.45	5	8	3	.90	.92	.90
herbicide	.44	.58	<.01	5	7	2	.91	.96	.91
mowed	.41	.46	.58	6	8	4	.91	.96	.91
DIPTERA									
control	.25	.29	.32	3	5	3	.80	.96	.67
herbicide	.28	.30	.28	3	6	3	.74	1.00	.59
mowed	.26	1.00	.28	3	5	2	.85	1.00	.93
HYMENOPTERA									
control	.66	.70	.67	6	10	6	.80	.90	.86
herbicide	.64	.71	.95	6*	16	12	.80	.95	.88
mowed	.65	.57	.75	5*	16*	7	.77	.91	.88
ACARI									
control	.68	–	–	7	1	0	.77	–	–
herbicide	.66	<.01	–	7	3	0	.76	1.00	–
mowed	.62	<.01	–	7	3	0	.77	1.00	–
ARANAE									
control	.33	.38	.86	4	4	8	.94	.79	.95
herbicide	.30	.48	.75	3*	10	6	.95	1.00	.97
mowed	.39	.48	.61	5*	10*	5	.94	1.00	.87

[a] An asterisk indicates that species richness differs significantly ($P < .05$) between adjacent years.

also reported by Bulan and Barret (1971), as homopteran species increased in abundance during grassland regrowth.

Herbicide-treated sites had increases in population densities, probably due to the same phenomenon as in mowed sites. That is, some regrowth and understory herbaceous plants that had been hindered by the overstory became available to forbivorous arthropods. Ovington et al. (1963) showed that an overstory canopy could decrease understory plant biomass in forests.

An increase in collembolan population density and richness in herbicide-treated sites may have followed an increase of fungi, resulting from degradation of the herbicide. The degradation of 2,4-D has been shown to increase fungal growth (Klingman and Ashton 1982), and the increased food resources for collembolan fungivores may have aided population growth (Poole 1959). Reproductive rates can increase when increases of food resources are made available (Emilen 1984). Longstaff (1976) showed that intense competition can change a collembolan system to the point that only a few species will become dominant. Greater competition may have occurred when the densities of decomposer collembolan species increased through the summer. The recovery year began with a high density, possibly due to either a carryover from the treatment year or high reproduction in spring. Increases in population densities in mowed sites may have resulted from the influx of detritus available to litter-inhabiting and litter-consuming springtails.

Psocopterans were not a major part of the arthropod fauna until the third year of the study in either unmanaged or managed sites. The increase at the end of the treatment year was reflected in the recovery year by a high density in unmanaged sites, with a population peak in midsummer. This order of arthropods feeds upon fungi and small remains of other arthropods (Borror et al. 1981). The population increase by the third year may have been enhanced by an increase of fungi resulting from 2,4-D degradation.

Thysanura had low population densities and richness throughout the three-year study in unmanaged sites. Populations did not respond to herbicide treatment until the recovery year. The rate of population growth may have increased as more fungal resources became available via 2,4-D degradation.

Hemipteran populations were not a major part of the fauna until the third year. The low diversity and density of Hemiptera for the first two years is difficult to explain, inasmuch as Kraft (1960) showed a large diversity of this order occurring in a sagebrush community. However, Kraft's (1960) study site was several thousand feet lower than our site, and this discrepancy in elevation may have accounted for the difference in population parameters. Although seed production was not assessed, this may also have been a reason for low hemipteran density. There were several species of seed-eating pentatomids within each treatment, but populations did not exceed 5% of the total hemipteran fauna. These insects have been associated with regulating bitterbrush seed production (Basile et al. 1964).

Homoptera had peak densities in midsummer, as was seen in grassland studies by Evans and Murdoch (1968) and McDaniel (1971). The decrease in population evenness by midsummer indicated that a few species reached relatively high population densities. This indicated a significant homopteran population restructuring during peak plant biomass. Foliage population densities decreased significantly with disturbance; however, diversity, richness, and evenness all increased. These data indicate that effects from habitat disturbance may have created more niches in this habitat. Homopteran diversity data from this study agreed with results of a study by Southwood et al. (1979), which showed that insect diversity declined after 16 months during secondary succession in most habitats.

Several predatory coleopteran species were dominant in the litter of unmanaged sites during most of each summer. The loss of hiding places in foliage or the decrease in prey density due to disturbance may have decreased coleopteran richness. There was only one beetle species in the foliage component after mowing, as compared with seven before habitats were disturbed. However, by the end of the treatment year, richness and density greatly increased. Richness nearly reached the level of pretreatment, and density increased by sixfold. This would indicate that foliage coleopteran populations can reestablish in a short period of time. Reestablishment persisted until late summer of the recovery year, after which time density and diversity again declined.

Dipteran populations peaked when both prey and plant resources were at a maximum, as has been found in other studies (Southwood et al. 1979, Lawton 1978). Litter dipteran populations were affected in herbicide-treated sites. This was also seen in a study by Ripper (1956) in which pesticides destabilized systems. Populations from the foliage component appeared to have moved into the litter during the treatment year. By the recovery year, species richness in foliage returned to the level found in the baseline year, although density remained lower than in any previous year.

The general decline in density of foliage Hymenoptera following brush management may have been due to a reduction in resources available to ants. Ant species are primarily seed gatherers, and, following treatment, seeds were not readily available. There was also a decline in the diversity of ant species in midsummer. A phenology study in Wyoming by Fisser (1984) showed that plants in sagebrush habitats produce seed in either early or late summer. Ant species present in midsummer were composed of generalist feeders and honeydew-feeding species. The increase in honeydew-feeding ant species coincided with an increase of aphids. Mowing was more disruptive than herbicide applications to plant structure (i.e., protective sites declined [Juniper and Southwood 1986]), and the resultant decline in homopteran densities was reflected by decreases in ant populations. In the recovery year, plant regrowth was seen throughout the mowed sites, with a concomitant increase in ant population indices in foliage and a decrease in litter. Thus, ant populations apparently moved back into the foliage component of disturbed sites.

The order Acari comprised the highest percentage of individuals in the litter component. Evenness decreased only slightly while richness decreased markedly in the recovery year in unmanaged sites, indicating that with fewer species in the habitat, there was a more balanced distribution of individuals among species. Herbicide-treated sites had an increase of mite populations within a month of habitat spraying. This density increase may have resulted, as in other fungivorous arthropods, from the consequences of 2,4-D degradation. Dindal et al. (1975) saw a decrease in richness of mites when a grassland habitat was disturbed. Their work with orbatid mites indicated, as did this study, that simplification within the acarine community resulted from reduction of richness due to management practices. The recovery year had increases in ecological parameters of foliage mites, which may have been initiated by overcrowding in litter, to the point that mites began to move toward areas of low density. Movement of mites from a high-density to a lower-density habitat has been shown to occur in other systems (Morris 1971, Varley et al. 1973). Orbatid mites, which comprised a large portion of the mite community, colonized disturbed habitats, and new species of orbatids also appeared in disturbed sites. This type of colonization was seen by Dindal et al. (1975) in disturbed old-field habitats.

Populations of Aranae in foliage fluctuated in density, diversity, and richness. One possible explanation is the normal fluctuation that occurs as predator populations track prey populations (Emilen 1984).

ACKNOWLEDGMENTS

We thank J. C. Burne for assistance with taxonomic identifications, C. C. Burkhardt for assistance with pesticide applications, and P. Lew for field and laboratory assistance. This project was partially funded by USDA-CSRS Grant 85-CSRS-2-2702.

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DEMOGRAPHIC CHARACTERISTICS OF AMERICAN MARTEN POPULATIONS IN JACKSON HOLE, WYOMING

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ABSTRACT.—Some American marten population characteristics (numbers, density, body weights, sex and age ratios, natality, mortality-survivorship, immigration-emigration, home ranges) were studied at four sites in the southern part of the Greater Yellowstone Ecosystem, Teton County, Wyoming, in 1975–1979. Ninety-eight different martens were examined. Males ($n = 25$) weighed 1,111 g (± 110 SD, range 875–1,235), whereas females ($n = 17$) averaged 743 g (± 83 SD, range 600–900). Live-trapping showed sex ratios of 1.5M:1.0F, whereas carcasses showed 3.0M:1.0F. Of 27 males that were aged, 12 (44%) were less than 1 year old and 2 were 9–10 years old. Of 10 females, 6 were less than 1 year old and 1 was 12–13 years old. The mean length of time a male was present on the major study area was 144 days (± 266 SD, range 1–1,364), and for females it was 145 days (± 45 SD, range 1–560). Home ranges for six males averaged 3.2 km^2 (± 20 SD, range 0.7–5.8) on the main study area. Some management implications are given.

American martens (*Martes americana vulpina*) are medium-sized, solitary carnivores that were historically abundant in North American mature and old-growth coniferous forests (Strickland and Douglas 1987, Clark et al. 1987). Martens have been significantly reduced over the last 100+ years by extensive habitat alteration and overexploitation and have been completely extirpated in some portions of their range. Today, most states and Canadian provinces classify martens either as furbearers subject to regulated trapping or as a rare and protected species. Reintroductions to unoccupied former range in Saskatchewan, Ontario, Manitoba, British Columbia, Michigan, Wisconsin, Arkansas, South Dakota, Oregon, Washington, and Colorado in the last few decades have been relatively successful (Richardson et al. 1986: 171).

Martens are relatively abundant in the Greater Yellowstone Ecosystem (GYE) of northwestern Wyoming, southeastern Idaho, and southern Montana. This is largely the result of relatively little habitat alteration (e.g., timber harvests) and limited trapping occurring in this mostly intact biogeographic area, which includes Yellowstone National Park, Grand Teton National Park, and seven national forests. However, because small marten populations are susceptible to local extinction, the species has been classed as "sensitive" and as an "indicator species" on Bridger-Teton, Targhee, and Gallatin National Forests under the 1976 National Forest Management Act. To aid marten conservation and management, we present data on population characteristics from four sites in Teton County, Wyoming, in the southern part of the GYE.

STUDY AREA

The general study area encompasses Jackson Hole in Teton County, Wyoming, and largely comprises Grand Teton National Park and Bridger-Teton National Forest. Four study sites within this area are compared in Table 1: Grand Teton National Park (GTNP), Bridger-Teton National Forest (BTNF), Teton Wilderness (TW), and Targhee National Forest (TNF). Live martens were studied in GTNP and BTNF, whereas trappers provided marten carcasses from TW and TNF.

The climate is characterized by low mean annual temperatures and long, cold winters with deep snows (U.S. Dept. Commerce Weather Bureau 1975). Geomorphology and physiography of the area are described by Love and Reed (1968); soils are described by Young (1982). Elevations range from 1,964 m to 4,185 m above sea level. Vegetation is largely coniferous forests and shrub-grasslands (Reed 1952).

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TABLE 1. Comparison of four American marten study sites, Teton County, Wyoming.

Study area	Size (ha)	Physiography	Vegetation	Study history, methods, authors
Grand Teton National Park	1,554	flat bench on east slope of Teton Mts.; 2,200 m	lodgepole pine (*Pinus contorta*)	(39 mo) Apr 1975–Aug 1976; May 1977–Apr 1979
			spruce/fir (*Picea engelmannii*, *Abies lasiocarpa*)	live trapping/radiotelemetry Hauptmann (1978), Clark (1984)
Bridger-Teton National Forest	646	north slope, Topping Lake area; 2,300–2,700 m	Douglas fir (*Pseudotsuga menziesii*)	(6 mo) Sept.–Oct 1974; June–Sept 1976 live trapping/radiotelemetry
			lodgepole pine	Campbell (1979), Clark (1984)
			spruce/fir	
Teton Wilderness	2,300	varied, mountainous; 2,300–2,800 m	Douglas fir	(6 mo) fall–winter 1975–1977
			lodgepole pine	skulls from trappers
			spruce/fir	
Targhee National Forest	5,100	west slope of Teton Mts.; 2,000–2,600 m	Douglas fir	(6 mo) fall–winter 1975–1977
			lodgepole pine	skulls from trappers
			spruce/fir	

METHODS

Marten population data come from live-trapped and radio-collared martens and from trapper-harvested carcasses collected from 1975 through 1979. Double-door National live traps were set in lines with traps about 0.2 km apart and checked daily for 7–10 days each month. Topography, vegetation, and marten signs determined trap sets. Trap locations were plotted on topographic maps. Captured martens were weighed to the nearest 25 g, aged, sexed, and examined; capture date and location were recorded. Animals were identified using color-coded, numbered ear tags and distinguishing characteristics (e.g., color pattern of venter, broken or discolored teeth, scars, etc.) when possible. Some martens were radio-collared with transmitters (model #SB2 IV) and monitored with a receiver (model #LA 12) and hand-held Yagi antennae (AVM Instrument Co., Dublin, California). Information on home ranges was obtained from live-trapping and telemetry. Home ranges were determined in two ways: (1) joining the outer points of locations or captures (minimum polygon method), and (2) measuring the greatest distance between points of capture or telemetry-determined locations and using this measure as the diameter of a circle to give an area estimate (range length method; Stickel 1954).

Marten skulls of known sex were collected from commercial trappers and cleaned in a dermestid beetle colony at Idaho State University. A canine was removed from each skull and sectioned, and cementum annuli were counted following Kelly (1977) and Strickland et al. (1982) to provide ages.

RESULTS

Trapping efforts, marten numbers, population densities, body weights, sex and age ratios, survivorship, residential status, immigration and emigration characteristics, and home ranges are summarized for the four study sites in Table 2. In all, 98 different martens were examined. The GTNP site yielded 46% of all martens, and much of the following information was collected from this population.

TABLE 2. American marten population characteristics, Teton County, Wyoming.

					Residential status[4] [x days (± SD) range]				
Study area	No. different marten	Sex ratio (M:F)	Age[1] [x yrs (± SD) range]	Length of time in study area [x days (± SD) range]	Resident	Temporary resident	Transient	Young born on site	Unknown
Grand Teton National Park	45	1.5:1.0	M 2.3 (± 1.2) 1–5 n = 3 F 2 n = 1	M 144 (± 266) 1–1,364 n = 13 F 145 (± 145) 1–560 n = 5	M 281 (± 332) 90–1,364 n = 13 F 266 (± 159) 145–560 n = 5	M 28 (± 16) 13–62 n = 7 F 46 (± 16) 33–69 n = 3	M 2 (± 1.6) 1–5 n = 5 F 1 (± 0.4) 1–2 n = 9	3 M	—
Bridger-Teton National Forest	17	1.4:1.0	—	—	6 M 3 F	0 M 1 F	3 M 1 F	2 M 0 F	1
Teton Wilderness[2]	16	3.0:1.0	M 5.4 (± 2.8) 0–5 n = 11 F 7.2 (± 4.7) 0–13 n = 4	—	—	—	—	—	—
Targhee National Forest[3]	20	3.0:1.0	M 6.0 (± 4.9) 0–7 n = 15 F < 1 yr n = 5	—	—	—	—	—	—
TOTALS OR MEANS	98	1.9:1.0	—	—	—	—	—	—	—

[1] Based on cementum layers.
[2] Unexploited population trapped for first time 1975.
[3] Heavily exploited population trapped annually.
[4] Resident (90+ days), temporary resident (7–89 days), transient (less than 7 days).

TRAP EFFORT

Trapping efforts on the GTNP and BTNF sites totaled 10,377 trap-days (one trap-day equals one trap set for 24 hrs) and resulted in 590 total captures and a capture rate of 5.7 marten per 100 trap days. Capture rates were 5.9 per 100 trap-days in GTNP and 4.9 per 100 trap-days in BTNF. The mean number of captures per individual and the number of different locations per individual varied between the two study sites (Table 3). Few previously untrapped marten were captured after 10 consecutive days of trapping (Fig. 1).

Numbers and Density

The 1,554-ha GTNP site showed a mean monthly population of 5.3 martens (± 2.2 SD, range 2–10) over 39 months (Fig. 2). Mean monthly populations, including transients, peaked in October, November, and December of each year (Fig. 3). The monthly mean for males in GTNP was 3.8 (± 1.8 SD, range 1–9), and for females it was 1.5 (± 1.4 SD, range 0–5). The 646-ha BTNF site had a mean monthly population of 6.8 martens (± 2.2 SD, range 1–9) over a six-month period. The monthly mean for BTNF males was 4.3 (± 1.1 SD, range 1–5), and for females it was 3.7 (± 0.9 SD, range 0–4).

Densities on the GTNP site, based on home range estimates, averaged one marten (males only) per 3.2 (± 2.0 SD) km^2. The BTNF site showed one male per 1.0 (± 0.8 SD) km^2 and one female per 0.3 (± 0.3 SD) km^2.

Body Weights

Body weights of martens fluctuated monthly (Fig. 4). For the GTNP site, 25 males caught for the first time averaged 1,111 g (± 110 SD, range 875–1,235), whereas 17 females averaged 743 g (± 83 SD, range 600–900). Females were 67% of the mean weight of males. For the BTNF site, 72 male weights (many weights of the same animal over successive trap-days) averaged 1,198 g (± 109 SD, range 875–1,450), whereas 24 females averaged 735 g (± 71 SD, range 650–875). Females were 61% of the mean weight of males.

Sex and Age Ratios

Sex ratios were nearly identical for GTNP (1.5M:1.0F) and BTNF (1.4M:1.0F), the two study sites sampled with live-traps. On the

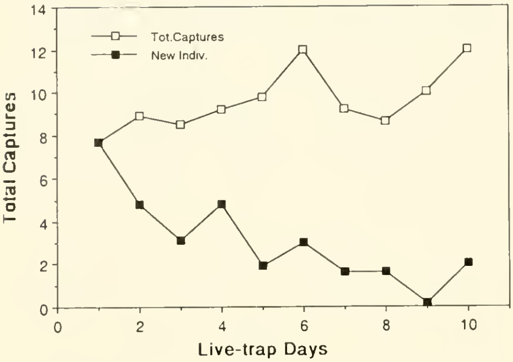

Fig. 1. Comparison of capture rates between total capture of marten and previously unmarked individuals on the Grand Teton National Park site, Teton County, Wyoming.

two study sites in which marten were harvested, the sex ratio was the same [3.0M:1.0F (Table 2)].

Age ratios were sampled via counts of cementum annuli on canine teeth (Table 2). Three of four male mortalities on the GTNP site averaged 2.3 years (± 1.2 SD, range 1–5), and a single female was 2 years old. Eleven males on the TW site averaged 5.4 years (± 2.8 SD, range 0–9), and 4 females averaged 7.2 years (± 4.7 SD, range 0–13). Fifteen males on the TNF site averaged 6.0 years (± 4.9 SD, range 0–7), and 5 females were all less than 1 year. Sex structure of the GTNP population varied monthly (Fig. 5); males were more numerous than females in 30 of the 39 months of study.

Mortality-Survivorship

The 27 males and 10 females from the GTNP, TW, and TNF sites whose ages were determined provided estimates of mortality-survivorship rates. Twelve males were less than 1 year old; five were 1–2 years old; three were 2–3 years old; one was 3–4 years old; two were 4–5 years old; one was 5–6 years old; one was 7–8 years old; and two were 9–10 years old. Six females were less than 1 year old; one was 1–2 years old; one was 5–6 years old; one was 8–9 years old; and one was 12–13 years old.

Immigration and Losses (Emigration and Mortality)

Marten losses from live-trapped study sites cannot be distinguished by cause (i.e.,

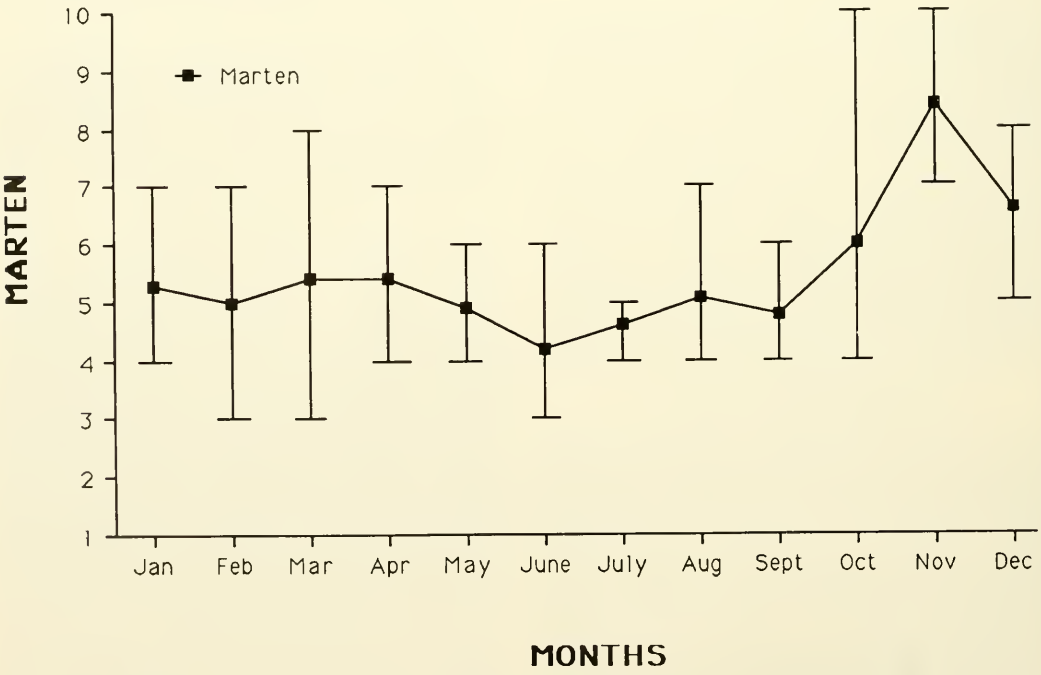

Fig. 2. Monthly mean numbers of American marten on the Grand Teton National Park study site, Teton County, Wyoming.

TABLE 3. Trap effort and capture rates for American marten, Teton County, Wyoming.

Study area	Trap-days[1]	No. different marten captured	Total captures	Martens per 100 trap-days	Captures per individual [$\bar{x}$ (± SD) range]	No. different locations [$\bar{x}$ (± SD) range]
Grand Teton National Park	8,390	45	493	5.9	11 (± 14) 1–96	5 (± 7) 1–27
					M 12 (± 19) 1–96	M 5 (± 6) 1–27
					F 9 (± 17) 1–76	F 3 (± 4) 1–12
Bridger-Teton National Forest	1,987	17	97	4.9	6 (± 6) 1–21	3 (± 2) 1–9
					M 7 (± 7) 1–21	M 3 (± 2) 1–9
					F 3 (± 3) 1–9	F 2 (± 1) 1–9
TOTALS OR MEANS	10,377	62	590	5.7	$\bar{x}$ = 8.5 $\bar{x}$ = 9.5 $\bar{x}$ = 6.0	$\bar{x}$ ± 4.0 $\bar{x}$ = 4.0 $\bar{x}$ = 2.5

[1] Trap-days are traps set for 24 hours.

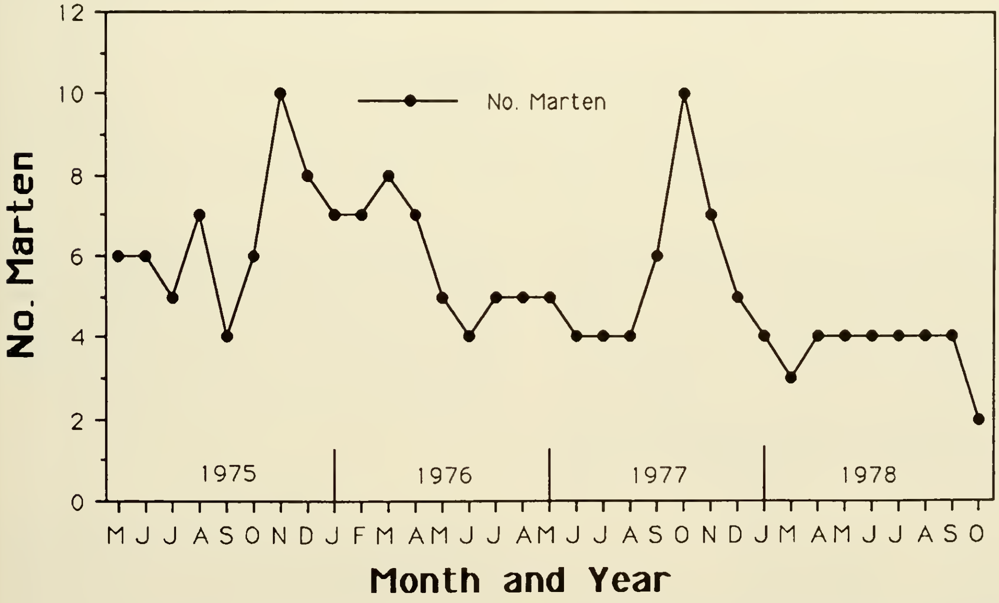

Fig. 3. Number of American marten captured by month on the Grand Teton National Park study site, Teton County, Wyoming.

emigration or death), and so are treated simply as losses. Further, only the GTNP site was trapped long enough to obtain data on the movement of martens into or out of the site (Table 4). Between 1975 and 1979, male losses occurred 11% more often than female losses. Only 3% of all marten losses occurred between January and March, while 48% occurred during October and November. between August and November, 68% of all male immigration and 79% of all male losses were observed. In contrast, 67% of all female immigration and 50% of all female losses occurred during the same months. Monthly marten immigration rates were similar to loss rates during each given month.

The mean length of time a given male was present on the GTNP was 144 days (± 266

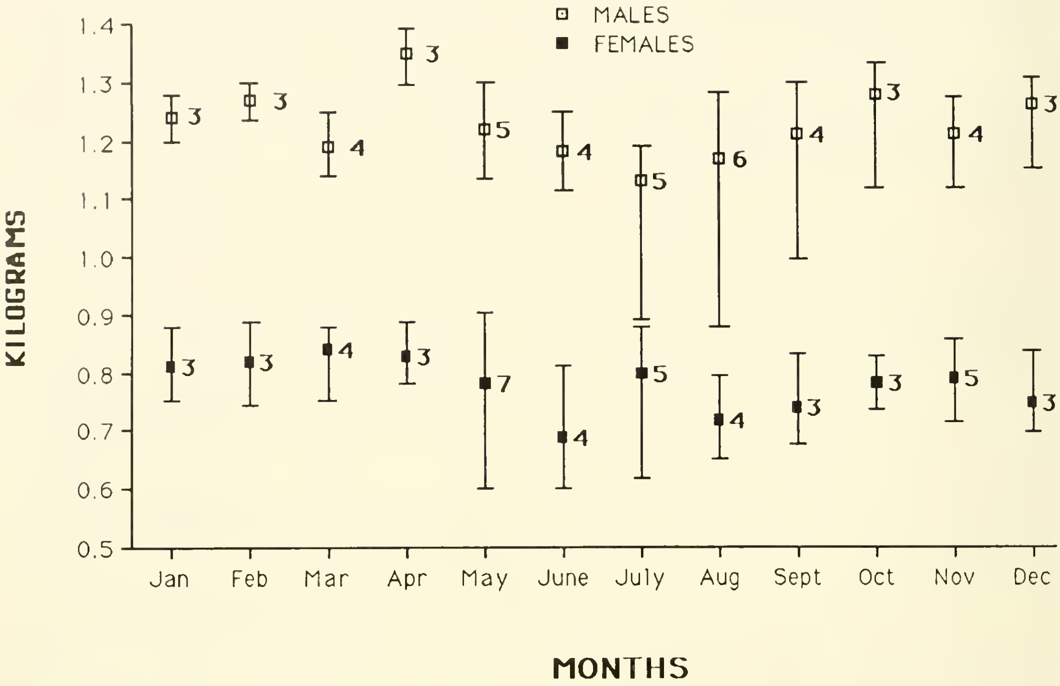

Fig. 4. Mean body weights and weight ranges of male and female American marten on the Grand Teton National Park study site, Teton County, Wyoming.

SD, range 1–1,364); for females it was 145 days (± 145 SD, range 1–560; Table 2). Martens were classified as residents if they remained on the site over 90 days, as temporary residents (8–89 days), and transients (< 7 days), following Hawley and Newby (1957). Table 3 shows the durations of residents, temporary residents, and transients on the site. Less than half the GTNP population were residents.

Home Ranges

Males on the GTNP and BTNF study sites had different home range sizes (Table 4). Six GTNP male home ranges averaged 3.2 km^2 (± 2.0 SD, range 0.7–5.8), whereas six BTNF male home ranges averaged 1.0 km^2 (± 0.8 SD, range 0.1–2.4). Female home ranges were estimated only on BTNF, where three females occupied a mean of 0.3 km^2 (± 0.3 SD, range 0.1–0.7). On the BTNF site, male home ranges were about three times larger than female home ranges; insufficient data were collected on GTNP females to make a similar comparison.

Home range estimates varied depending on the method of calculation (Table 5). On the GTNP, estimates of two male home ranges were 5.4 and 5.8 km^2, based on live-trapping and radio-telemetry locations. In contrast, four other males had home ranges of 3.3, 3.1, 0.7, and 0.7 km^2, based only on captures.

DISCUSSION

Capture rates for Teton County martens of 5.9 and 4.9 per 100 trap-days were less than recorded elsewhere. Miller et al. (1955) captured 7.0 martens per 100 trap-days, and Hawley and Newby (1957) captured 13.1 martens per 100 trap-days. This may be a result of trapping techniques or differences in marten behavior or habitat.

Teton County martens showed pronounced sexual dimorphism in body weight, as they do throughout North America (Clark et al. 1987). Teton County females weighed about 65% of the weights of males.

Sex ratios in Teton County martens were nearly identical in the two live-trapped samples (1.5M:1.0F) and the two harvested samples

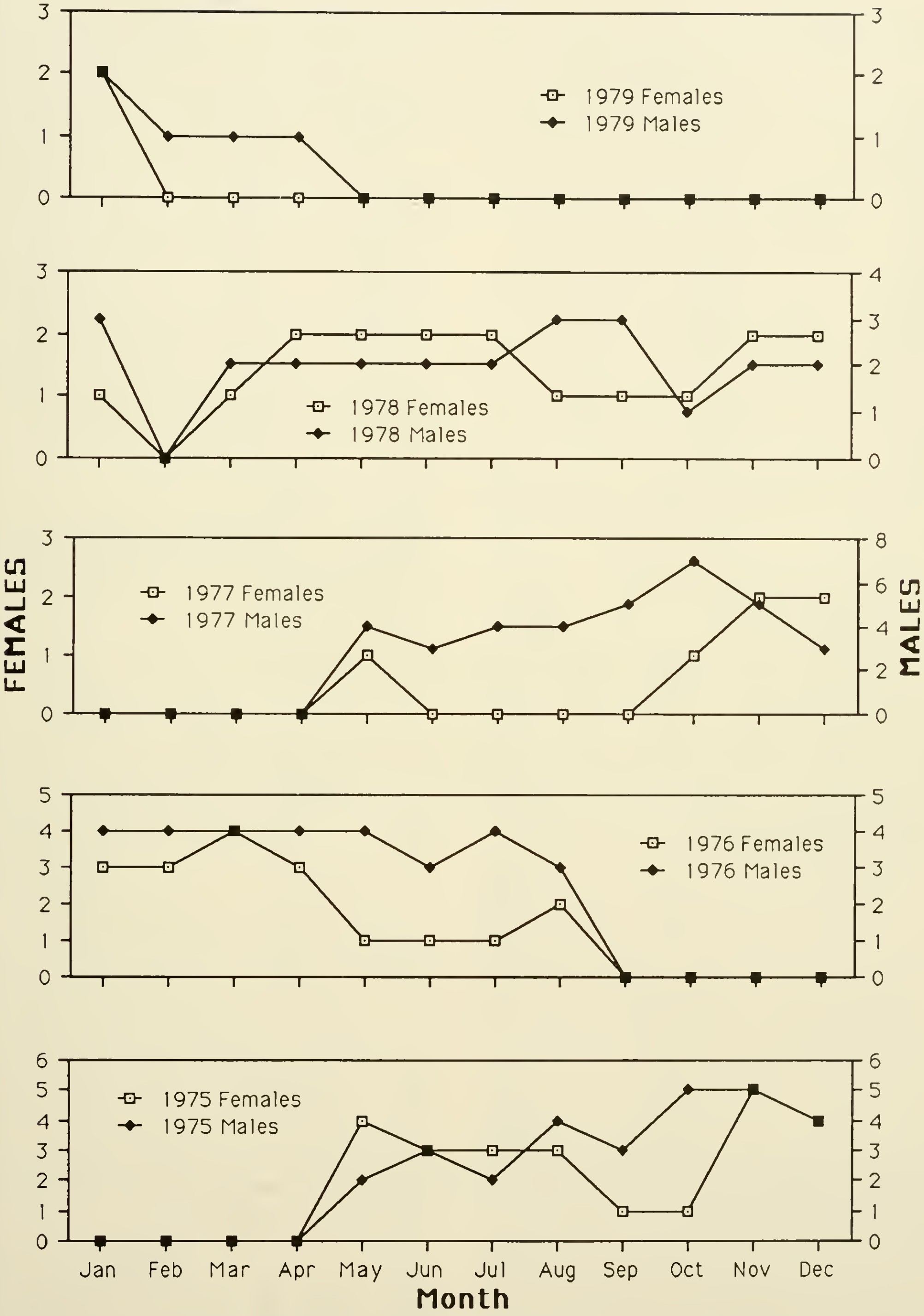

Fig. 5. Sex structure of captured American marten on the Grand Teton National Park site, Teton County, Wyoming.

TABLE 4. American marten immigration and loss statistics for the Grand Teton National Park population, Teton County, Wyoming.

	Immigration		Losses		
Month	Male (%)	Female (%)	Male (%)	Female (%)	Totals (%)
January	0	0	0	1 (8.3)	1 (1.6)
February	0	0	0	0	0
March	0	1 (7.8)	0	1 (8.3)	2 (3.1)
April	0	2 (15.4)	0	3 (2.5)	5 (7.8)
May	2 (10)	1 (7.8)	3 (15.8)	1 (8.3)	7 (10.9)
June	2 (10)	0	0	0	2 (3.1)
July	2 (10)	0	1 (5.3)	0	3 (4.7)
August	3 (15)	1 (7.8)	4 (30.1)	1 (8.3)	9 (14.1)
September	3 (15)	0	1 (5.3)	0	4 (6.3)
October	5 (25)	1 (7.8)	7 (36.8)	1 (8.3)	14 (21.9)
November	2 (10)	6 (46.1)	3 (16)	4 (33.3)	15 (23.4)
December	1 (5)	1 (7.8)	0	0	2 (3.1)
TOTALS	20 (31.3)	13 (20.3)	19 (29.7)	12 (18.7)	64 (100)

TABLE 5. Home range estimates for American marten, Teton County, Wyoming.

			Home range estimates	
Study area	No. locations	No. days	Minimum area (km)[2]	Range length (km)[3]
Grand Teton National Park				
Male No.				
17	14	78	3.3	—
25	16	74	0.7	—
26	9	66	0.7	—
29	13	141	3.1	—
30	34	160	5.4[1]	—
100	53	164	5.8[1]	—
Means (± SD)	23 (± 15)	114 (± 42)	3.2 (± 2.0)	—
Bridger-Teton National Park				
Male No.				
4	7	16	1.6	1.4
5	4	378	0.1	0.4
7	14	365	0.2	0.6
8	31	385	1.6[1]	1.4[1]
12	31	220	2.4[1]	1.8[1]
13	4	80	0.4	0.7
Means (± SD)	15 (± 12)	241 (± 148)	1.0 (± 0.8)	1.1 (± 0.5)
Females No.				
1	16	347	0.7[1]	1.0[1]
9	2	320	0.2[1]	0.6[1]
10	2	263	0.1	0.4
Means (± SD)	7 (± 7)	310 (± 35)	0.3 (± 0.3)	0.6 (± 0.2)

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[1] Both trap and telemetry; all other martens, traps only.
[2] Based on minimum polygon method.
[3] Based on range length as diameter of a circle.

(3.0M:1.0F), but differed considerably between live- and kill-trap samples. Similar sex ratios (two to three times as many males as females) have been reported elsewhere. Twining and Hensley (1947), DeVos and Guenther (1952), Yeager (1950), Lensink (1953), and DeVos et al. (1959) found males predominant in harvest samples. The preponderance of males in these samples may be accounted for by the larger home ranges of males and by the extensive wandering of juvenile males in search of unoccupied home ranges—both characteristics making them more likely to encounter traps (Quick 1956a, 1956b, Yeager 1950). Male predominance in catches may be accentuated by a greater mortality in females and juveniles during periods of prey scarcity and the more vulnerable energy balance of females (Hawley and Newby 1957, Weckwerth and Hawley 1962). However, the sex ratio of martens at birth is not significantly different from 1:1 (Brassard and Bernard 1939, Markley and Bassett 1942, Ritchie 1953).

Forty-four percent of 29 male Teton County martens, nearly all of which were trapper-harvested, and 60% of 10 females were less than 12 months old. Strickland et al. (1982) noted that 60–80% of trap-harvested martens are young-of-the-year. Lensink (1953) found that the proportion of adults caught in hunter harvests is higher in newly or lightly trapped areas than on heavily trapped lines. The oldest marten we caught showed 13 annuli, the same as the oldest marten that Strickland et al. (1982) reported in a hunter-harvest sample of 718 from Ontario. Martens are known to live up to 15 years in captivity (Strickland et al. 1982).

No data were gathered on natality rates from the Teton County martens. A few young marten were identified each summer and fall, but aging techniques in the field are limited. According to Strickland et al. (1982) martens produce a litter of three or slightly less annually.

Martens are taken by several avian and mammalian predators (Clark et al. 1987), but predation is not thought to cause significant impact on wild populations (Raine 1981). No predations were observed in this study. Strickland et al. (1982) found that about 50% of males and 54% of females died before reaching 12 months of age. For older martens, 20% of males and 15% of females died between 1 and 2 years of age; 13% of males and 12% of females died between the age of 2 and 3 years; few wild marten live over 4 years. The limited survivorship data from Teton County show a similar pattern.

Numerous martens immigrated into and emigrated from the two Teton County live-capture study sites. Many of these movements were in the fall, and males tended to move more often than females. In the GTNP site over the four years of study, overall marten numbers immigrating or emigrating were almost equal. Similar patterns have been seen elsewhere (DeVos 1951, Hawley and Newby 1957, Francis and Stephenson 1972). Weckwerth and Hawley (1962) found juvenile male dispersal movements of 27–40 km. No actual dispersal movements were recorded for Teton County martens, but some probably occurred and went undetected.

Teton County martens resided on the study sites for different lengths of time. On the GTNP site, 43% of the martens were residents, 24% temporary residents, and 33% transients, whereas on the BTNF site, 67% were residents, 7% temporary residents, and 26% transients. In contrast, Weckwerth and Hawley (1962) found 47% residents, 21% temporary residents, and 32% transients in Montana. The greater percentage of residents on the BTNF site may be due to the site's better habitat quality (i.e., spruce and fir forest as compared with lodgepole pine forest in GTNP).

Teton County males had home ranges of about 1.0 km^2 (± 0.8 SD) to 3.2 km^2 (± 2.0 SD), depending on site characteristics. Female ranges were about one-third the size of male home ranges. Most data for these estimates came from tag and recapture trap studies. Elsewhere, live-capture studies have shown home range size calculated by the minimum area method to be 2–3 km^2 for males and 1 km^2 for females, whereas radiotelemetry studies have shown ranges of 10–20 km^2 for males and 3–6 km^2 for females (Clark et al. 1987).

Because home ranges overlap, densities can be relatively high. At peak densities in early fall when family groups disperse, there may be 1.2–1.9 martens per km^2 (Francis and Stephenson 1972, Soutiere 1979). This compares with the GTNP site, where male martens occurred at 1 per 3.2 km^2, and the BTNF site, where males occurred at 1 per 1.0 km^2. Differences are due to different temporal sampling and variations in habitat quality.

The American marten is vulnerable to local extinction as indicated by abundant historical data (e.g., Marshall 1942, Strickland and Douglas 1987, Clark et al. 1987). Understanding local and regional marten population characteristics is fundamental to sound management. The data presented here, combined with cited data, can be used to model the effects of systematic habitat changes (e.g., logging) and stochastic events (e.g., diseases) on small marten populations. Such a viability assessment can estimate extinction probabilities of marten populations of various demographics. Viability assessment, determination of area requirements, and careful habitat management are essential for conservation of this important forest carnivore and indicator species on national forests in the Greater Yellowstone Ecosystem.

ACKNOWLEDGMENTS

Bob Wood, Bill Barmore, Pete Hayden, Denise Casey, Maria Casey, John Weaver, John Hoak, George Gruell, Jim Munsell, and Bill Green all aided this study. Their assistance is greatly appreciated. Grants from The National Geographic Society, National Park Cooperative Studies Unit, Grand Teton Natural History Association, and Bridger-Teton National Forest (all to TWC) made this study possible. Critical advice on the manuscript was given by William Zielinski.

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TERRESTRIAL VERTEBRATES OF SCOTTS BLUFF NATIONAL MONUMENT, NEBRASKA[1]

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ABSTRACT.—A survey of terrestrial vertebrates was conducted at the Scotts Bluff National Monument (SBNM), Nebraska, to determine species composition, relative abundance, and distribution by habitat of the existing amphibians, reptiles, birds, and mammals. Various sampling methods were used to detect animal species richness and to estimate population densities. The seven major habitat types at SBNM contained 4 species of amphibians, 8 reptiles, 96 birds, and 28 mammals. The only endangered or threatened species observed was a dead bald eagle (*Haliaeetus leucocephalus*). The racer (*Coluber constrictor*) and prairie rattlesnake (*Crotalus viridis*) were the two most abundant snakes. The prairie falcon (*Falco mexicanus*) was a common raptor that nested in Scotts Bluff. Sympatric populations of mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) appeared to be hybridizing. The riverine woodland contained the greatest number of fauna species with only 4% surface area of SBNM. Sharp-tailed grouse (*Tympanuchus phasianellus*) and pronghorn antelope (*Antilocapra americana*), absent from the Monument, are two potential native species for reintroduction.

Scotts Bluff National Monument (SBNM), located in the Nebraska Panhandle, is an area characterized by rolling, xeric, short- and mixed-grass prairie intermixed with rocky bluffs and dissected by the North Platte River. In 1820, Major Stephen H. Long, sent by the U.S. Congress, led an expedition along the Platte River to the Rocky Mountains. In his report of the expedition he called this area "The Great Desert." Although many of the large animals that Major Long encountered, such as pronghorn (*Antilocapra americana*), bison (*Bison bison*), and bighorn sheep (*Ovis canadensis*), are no longer present in the Nebraska Panhandle, the remainder of the fauna still may be found on protected land such as SBNM. Though small, SBNM has highly diversified habitat types. There are other protected public lands in the Panhandle of greater acreage, but no other land holding contains both riparian habitat of the North Platte River and pine-studded bluffs.

No wildlife inventory has been conducted at SBNM since its establishment in 1919. Baseline data are needed to give National Park Service resource managers a point of reference to determine true changes in the faunal communities and to document the existence of any threatened or endangered species. The only formal wildlife research conducted at SBNM prior to this study was a study on population ecology of the prairie vole (*Microtus ochrogaster*) (Meserve 1971) and another on population status of a newly established black-tailed prairie dog (*Cynomys ludovicianus*) colony (Franklin 1983, 1984). Our study involved inventorying the species composition of the existing amphibian, reptilian, avian, and mammalian species, and determining their relative abundance and distribution by habitat at SBNM.

STUDY AREA

SBNM covers 1,200 ha in Scotts Bluff County, Nebraska. It lies on the south side of the North Platte River, directly west of the Gering city limits. Scotts Bluff, elevation 1,417 m, is the major topographical feature. This redstone bluff rises 183 m above the surrounding terrain. On its summit are ponderosa pine (*Pinus ponderosa*) and Rocky Mountain juniper (*Juniperus scopulorum*), along with a sparse coverage of mixed-grass prairie species. Between Scotts Bluff and the river is a small area of badlands (bare ridges and valleys of eroding sandstone). Along SBNM's southern border is South Bluff, a segment of a long bluff that extends east and west through the county. The only water source, besides the adjacent North Platte River, is an irrigation canal that extends across the northern edge of SBNM (Fig. 1).

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[1] Journal Paper J-13179 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 2519.

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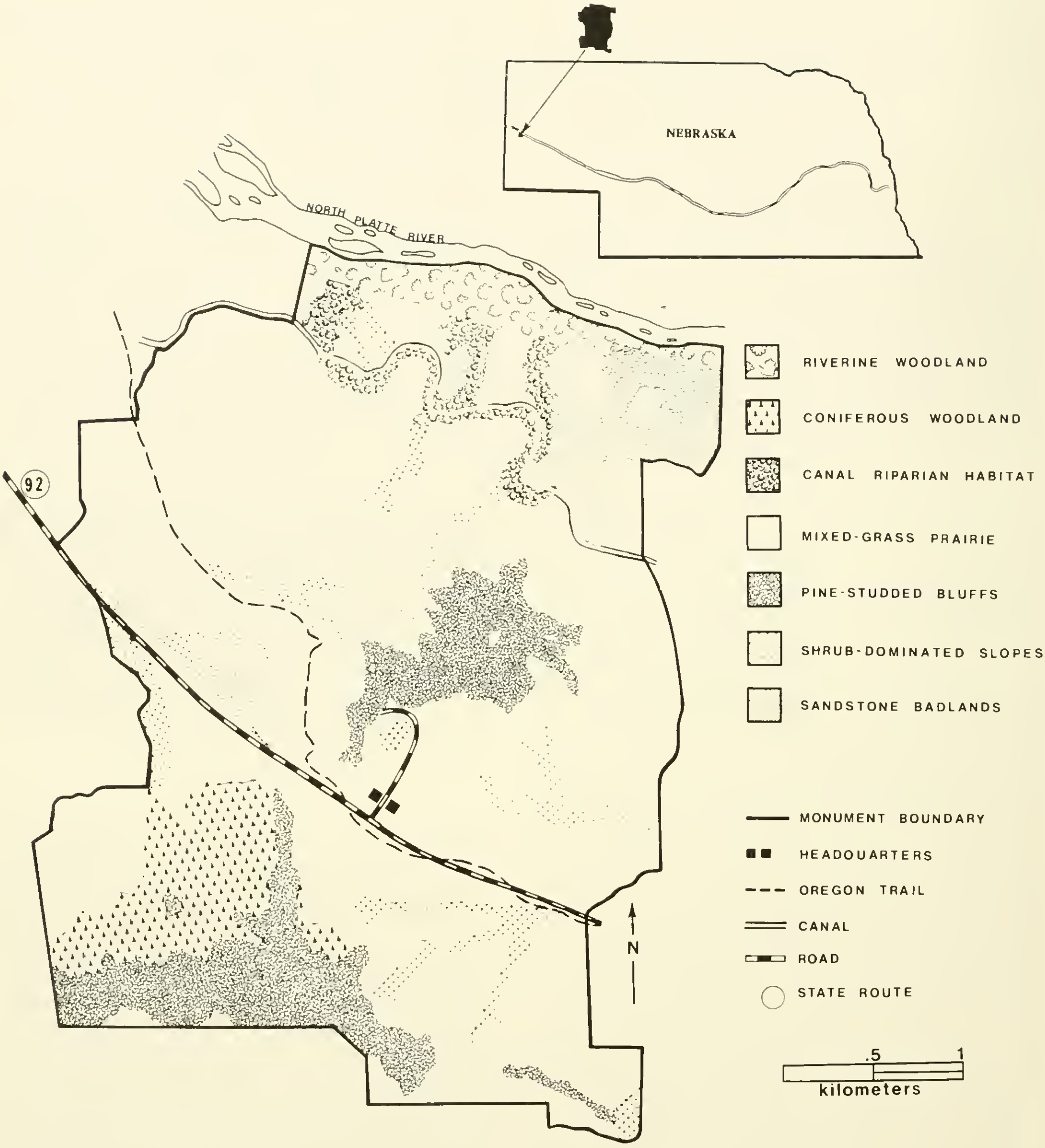
NEBRASKA
NORTH PLATTE RIVER
92
RIVERINE WOODLAND
CONIFEROUS WOODLAND
CANAL RIPARIAN HABITAT
MIXED-GRASS PRAIRIE
PINE-STUDDED BLUFFS
SHRUB-DOMINATED SLOPES
SANDSTONE BADLANDS
MONUMENT BOUNDARY
HEADQUARTERS
OREGON TRAIL
CANAL
ROAD
STATE ROUTE
N
.5
1
kilometers

Fig. 1. The seven major habitat types at Scotts Bluff National Monument, Nebraska.

We identified seven major habitats at SBNM: riverine woodland, coniferous woodland, mixed-grass prairie, canal riparian habitat, pine-studded bluffs, shrub-dominated slopes, and badlands (Fig. 1). Dominant tree species in the riverine woodland are cottonwood (*Populus deltoides*), willow (*Salix* sp.), box elder (*Acer negundo*), American elm (*Ulmus americana*), and green ash (*Fraxinus pennsylvanica*). Its understory includes *Carex* sp., *Bromus* sp., *Typha glauca*, and *Scirpus* sp. The coniferous woodland is dominated by ponderosa pine and Rocky Mountain juniper. Dominant grass and sedge species found in the mixed-grass prairie are needle-and-thread (*Stipa comata*), western wheatgrass (*Agropyron smithii*), downy brome (*Bromus tectorum*), side-oats grama (*Bouteloua curtipendula*), prairie sandreed (*Calamovilfa longifolia*), and threadlead sedge

(*Carex filifolia*). Common forbs and shrubs in the mixed-grass prairie are western wallflower (*Erysimum asperum*), prickly pear (*Opuntia compressa*), sweet clover (*Melilotus sp.*), kochia (*Kochia scoparia*), yucca (*Yucca glauca*), fringed sage (*Artemisia frigida*), sand sagebrush (*Artemisia filifolia*), winterfat (*Ceratoides lanata*), rubber rabbitbrush (*Chrysothamnus nauseosus*), skunkbush sumac (*Rhus trilobata*), and snowberry (*Symphoricarpos albus*) (Stubbendieck et al. 1986). Dominant tree species in the canal riparian habitat are cottonwood and willow; major shrubs are choke cherry (*Prunus virginiana*), snowberry, and *Ribes* sp.; the most common understory plant is poison ivy (*Toxicodendron rydbergii*). The pine-studded bluffs are dotted with ponderosa pine and Rocky Mountain juniper. Shrub-dominated slopes are primarily covered with skunkbush sumac and Rocky Mountain juniper. Though the badlands are predominantly bare rock, depressions and drainages contain limited cover of *Carex* spp., downy brome, rubber rabbitbrush, and willow.

Except for a small portion of land (in the extreme northwest corner) purchased in 1970, all vegetation has been protected from grazing by domestic animals since the 1930s. Average annual precipitation from 1978 through 1987 for Scotts Bluff County was 43.50 cm. Over 50% of the precipitation occurred during spring and early summer in the form of violent but brief thundershowers (Meserve 1971). Above-normal rainfall occurred during two years of this survey—55.22 cm in 1986 and 59.03 cm in 1987.

METHODS

Amphibians and reptiles were sampled with two 1 × 15-m drift fences made of aluminum flashing (Vogt and Hine 1982, Campbell and Christman 1982). One was placed in a wet meadow next to the canal and another in mixed-grass prairie. Pitfall traps were located on each end, and one funnel trap was located at the middle of each side of the fence. Traps were left opened and checked every other day from 24 April to 24 July 1987.

Three permanent line transects (1,400 m) were established to estimate avian species density and diversity (Shannon and Weaver 1964) in three selected habitat types (canal riparian habitat, mixed-grass prairie, and shrub-dominated slopes). Each transect was walked six times during early morning and evening hours in July 1986. Perpendicular distances from the transect were estimated for all visual and auditory avian detections (Burham et al. 1980, Mikol 1980, Emlen 1971).

Small mammals were surveyed in a permanent trapping web and also along various linear transects placed in all habitat types. The 4-ha trapping web consisted of 68 Sherman live traps and 32 pitfall traps located on 16 equidistant lines radiating from a center point (Wilson and Anderson 1985). Baited Sherman live traps and unbaited pitfall traps were opened during four-day trapping periods. Traps were set in early morning and left open for 24 hr. Trapping sessions in the trapping web were conducted 28 April and 11 June 1986 and 20 July 1987. Linear transects of either Sherman live traps (mark-recapture estimation) or snap traps (removal estimation) were placed throughout representative habitat types for four-day trapping periods: 26 June–12 August 1986 and 6 May–25 June 1987.

Prairie dogs were censused 12 June–5 October 1986 and 12 April–31 July 1987, with Tomahawk single-door and double-door live traps baited with rolled oats. All prairie dogs were ear tagged, fur dyed, weighed, sexed, and aged. Five permanent 0.4-ha plots were randomly selected throughout grassland sites to estimate pocket gopher densities on 1 July 1987. Estimation was based on freshly dug gopher mounds (less than one week old) in 10 subsamples (4 m^2 each) within each plot (Reid et al. 1966).

Deer and furbearer species were spotlighted from the canal road, one hour after sunset, three times during the summer 1987. Bats were mist-netted in the tunnels of the summit road from dusk to 0100 hr in June and July 1986 and 1987 seven times each year.

In addition to the previously defined methods, animals were recorded opportunistically during fieldwork June–August 1986, March–August 1987, and April–June 1988. Interviews with adjacent landowners helped assess the movement of animals on and off SBNM. Sightings by SBNM staff were verified and road kills collected within and adjacent to SBNM. Skulls, nests, and tracks also provided

TABLE 1. Definitions of abbreviations used in tables for residency status, habitat types, and relative abundance.

RESIDENCY STATUS
P = Permanent resident, breeding not documented
PB = Permanent resident, breeding documented
S = Summer resident (April–October), breeding not documented
SB = Summer resident, breeding documented
W = Winter resident (October–April)
M = Spring or fall migrant
T = Transient, present for only short duration

HABITAT TYPES
RW = Riverine woodland
CW = Coniferous woodland
CRH = Canal riparian habitat
MGP = Mixed-grass prairie
PSB = Pine-studded bluffs
S = Shrub-dominated slopes
B = Sandstone badlands

RELATIVE ABUNDANCE
A = Abundant
C = Common
U = Uncommon
R = Rare

useful information on the existing fauna. Taxonomic nomenclature for the herpetofauna was from Lynch (1985), birds from AOU checklist (1983), and mammals from Jones et al. (1983).

RESULTS

Abbreviations used in the species tables for habitat types, residency status, and relative abundance are defined in Table 1. A dead bald eagle (*Haliaeetus leucocephalus*) was the only endangered or threatened species found at SBNM during the two years of the study. The numbers of animal species detected include: 4 amphibians, 8 reptiles, 96 birds, and 28 mammals. These numbers reflect species observed, captured, heard, or positively identified by sign at least once during the two-year period. Other species that may have occurred at low abundance and went undetected will be discussed separately.

Amphibians

Amphibian species richness was low because of the absence of a permanent, nonflowing water source, important for breeding and egg deposition. The Woodhouse's toad (*Bufo woodhousii*), found on open grasslands, was the most common of the four species of amphibians (Table 2). The Great Plain's toad (*Bufo cognatus*) was found only on the lawns of the headquarters (Fig. 1). The western striped chorus frog (*Pseudacris triseriata*) and tiger salamander (*Ambystoma tigrinum*) were caught in pitfall traps of the drift fences on days immediately after heavy rains. There are no previous records of tiger salamanders in Scotts Bluff County (Lynch 1985).

Reptiles

Three turtle species were identified (Table 3). The painted turtle (*Chrysemys picta*) was found along the river and infrequently in the mixed-grass prairie. Ornate box turtles (*Terrapene ornata*), the most abundant turtles, were common in open grasslands, and are known to spend winters underground in burrows dug by turtles or rodents (Hammerson 1982). New county records were established for both the painted ornate box turtle and the spiny softshell turtle (*Trionyx spiniferus*) (Lynch 1985).

Of the five snake species identified (Table 3), the racer (*Coluber constrictor*), commonly referred to as a "blue" racer, and the prairie rattlesnake (*Crotalus viridis*) were the two most abundant snakes. Although both species were found in shrubs and dense grass during any part of the day, the prairie rattler was commonly associated with shorter, sparser vegetation than was the racer. The earliest sighting of a prairie rattler in 1987 was 29 April and, in 1988, 17 April. From mid-June through the first week of August 1986, 18 rattlesnakes were observed in separate areas located throughout SBNM. During this same period in 1987, 19 rattlesnakes were seen. Only perennially wet areas, such as those in the riverine woodland, seem to be avoided by rattlesnakes. Bull snakes (*Pituophis catenifer*) were found throughout SBNM where there was an abundant small mammal population. This is a new county record (Lynch 1985).

Birds

PELECANIFORMES, CICONIIFORMES, AND ANSERIFORMES.—Nine species from these orders were found (Table 4). The double-crested cormorant (*Phalacrocorax auritus*) was observed on the banks of the Platte River during the summer. Great blue herons (*Ardea herodias*) were seen frequently in the river and occasionally foraging in the canal. A pair of wood ducks (*Aix sponsa*) and ducklings were seen

TABLE 2. Amphibian species residency status, distribution by habitat, and relative abundance at Scotts Bluff National Monument. Abbreviations are explained in Table 1.

		Habitat types						
Common name *Scientific name*	Residency status	RW	CW	CRH	MGP	S	PSB	B
Tiger salamander *Ambystoma tigrinum*	PB	U		U	U			
Great Plains toad *Bufo cognatus*	PB				U			
Woodhouse's toad *Bufo woodhousii*	PB	C		C	C	U		U
Western striped chorus frog *Pseudacris triseriata*	PB	C		U				U

TABLE 3. Reptilian species residency status, distribution by habitat, and relative abundance at Scotts Bluff National Monument. Abbreviations are explained in Table 1.

		Habitat types						
Common name *Scientific name*	Residency status	RW	CW	CRH	MGP	S	PSB	B
Painted turtle *Chrysemys picta*	PB	C		C	U			U
Ornate box turtle *Terrapene ornata*	PB	C		C	C	U	U	U
Spiny softshell turtle *Trionyx spiniferus*	P	U						
Racer *Coluber constrictor*	PB	A	C	A	A	C	U	U
Bull snake *Pituophis catenifer*	PB	C	C	C	A	C	U	U
Plains gartersnake *Thamnophis radix*	PB	U		C	U			U
Common gartersnake *Thamnophis sirtalis*	PB	C		C	R			
Prairie rattlesnake *Crotalus viridis*	PB	U	C	U	A	C	C	U

consistently in the canal, but no nest was found. The mallard duck (*Anas platyrhynchos*) was the most abundant waterfowl species at SBNM and successfully nested in upland areas including the prairie dog colony.

FALCONIFORMES.—A total of nine raptor species was observed (Table 4). On 5 April 1988 an adult bald eagle was found dead next to the canal in the northwest corner of SBNM. The eagle had been dead less than one week when found, but the cause of death could not be determined from external examination. A necropsy performed at the National Wildlife Disease Laboratory in Madison, Wisconsin, showed that the eagle died of pulmonary hemorrhage, possibly caused by electrocution. The only raptor whose nesting has been confirmed at SBNM is the prairie falcon (*Falco mexicanus*). In 1986 five fledgings from two successful nests were seen, and in 1987 seven fledgings were produced from the same two nests. Sightings of fledgings were strong evidence that American kestrels (*F. sparverius*) and turkey vultures (*Cathartes aura*) nested within Scotts Bluff, although no nests were located. A pair of adult golden eagles (*Aquila chrysaetos*) were observed in a nest on South Bluff, but no young were observed. A pair of red-tailed hawks (*Buteo jamaicensis*) were consistently seen soaring over South Bluff riding thermals, though no nest was located.

GALLIFORMES.—The introduced ring-necked pheasant (*Phasianus colchicus*) was well established at SBNM. The adult male pheasant population was estimated to be 20–25 during the post-hatch period, May–June 1987. Hailstorms during the middle of the pheasants' 1987 nesting season caused

TABLE 4. Avian species residency status, distribution by habitat, and relative abundance at Scotts Bluff National Monument. Abbreviations are explained in Table 1.

		Habitat types						
Common name *Scientific name*	Residency status	RW	CW	CRH	MGP	S	PSB	B
Double-crested cormorant *Phalacrocorax auritus*	S	U						
Great blue heron *Ardea herodias*	S	C		U				
Snow goose *Chen caerulescens*	M							
Canada goose *Branta canadensis*	S	U						
Wood duck *Aix sponsa*	S	U		U				
Green-winged teal *Anas crecca*	S	U						
Blue-winged teal *Anas discors*	S	U						
Mallard *Anas platyrhynchos*	SB	C		C	U			
Common merganser *Mergus merganser*	S	U						
Turkey vulture *Cathartes aura*	SB		U		C		C	
Osprey *Pandion haliaetus*	T						R	
Northern harrier *Circus cyaneus*	P				U		R	
Swainson's hawk *Buteo swainsoni*	S		U		U			
Red-tailed hawk *Buteo jamaicensis*	P	U	U		U		U	U
Golden eagle *Aquila chrysaetos*	P		R		R		U	
Bald eagle *Haliaeetus leucocephalus*	M	R		R				
American kestrel *Falco sparverius*	SB	R	U	C	C	U	C	U
Prairie falcon *Falco mexicanus*	SB		U	R	C		C	
Ring-necked pheasant *Phasianus colchicus*	PB	U	U	U	C	C		R
Wild turkey *Meleagris gallopavo*	P	R		R				
Northern bobwhite *Colinus virginianus*	P			U	C	R		
Sora *Porzana carolina*	S	R						
Killdeer *Charadrius vociferus*	S	U		U	U			
Upland sandpiper *Bartramia longicauda*	S				R			
Franklin's gull *Larus pipixcan*	S				U			
Herring gull *Larus argentatus*	S				U			
Rock dove *Columba livia*	P						C	
Mourning dove *Zenaida macroura*	SB	C	U	C	C	C	U	R
Yellow-billed cuckoo *Coccyzus americanus*	S	R						
Barn owl *Tyto alba*	P				R	R		

TABLE 4 continued.

Great horned owl *Bubo virginianus*	PB	U	C	C	U	C	U	C
Burrowing owl *Athene cunicularia*	SB				C			
Short-eared owl *Asio flammeus*	P		R		R	R		
Common nighthawk *Chordeiles minor*	SB	U		U	C		C	U
Common poor-will *Phalaenoptilus nuttallii*	SB						U	
White-throated swift *Aeronautes saxatalis*	SB			U	U	U	A	
Chimney swift *Chaetura pelagica*	S				U		U	
Belted kingfisher *Ceryle alcyon*	S	U		U				
Northern flicker *Colaptes auratus*	SB	C		C	U	U		
Hairy woodpecker *Picoides villosus*	PB	U		U				
Downy woodpecker *Picoides pubescens*	PB	C		U				
Red-headed woodpecker *Melanerpes erythrocephalus*	S	R		R				
Western wood-pewee *Contopus sordidulus*	S		R	R				
Say's phoebe *Sayornis saya*	S	U	U	U	C	U		
Eastern kingbird *Tyrannus tyrannus*	SB	U	U	C	C	C	U	
Western kingbird *Tyrannus verticalis*	SB	U		U	C	U		
Horned lark *Eremophila alpestris*	P				U			
Northern rough-winged swallow *Stelgidopteryx serripennis*	S	C		C	U			
Bank swallow *Riparia riparia*	S	U						
Cliff swallow *Hirundo pyrrhonota*	SB	C		C	C			
Barn swallow *Hirundo rustica*	SB	C		C	C	U		
Blue jay *Cyanocitta cristata*	P	U		U				
Black-billed magpie *Pica pica*	PB	C	C	C	C	C	C	
American crow *Corvus brachyrhynchos*	P	R		R				
Black-capped chickadee *Parus atricapillus*	PB	C	C	C		U	C	U
Rock wren *Salpinctes obsoletus*	SB	U	U	U		C	A	C
House wren *Troglodytes aedon*	SB	A		A				
Eastern bluebird *Sialia sialis*	S	U						
Mountain bluebird *Sialia currucoides*	S					U		
Townsend's solitaire *Myadestes townsendi*	W		C					
Swainson's thrush *Catharus ustulatus*	M	U						
American robin *Turdus migratorius*	SB	C	A	C	C	C	U	C
Brown thrasher *Toxostoma rufum*	SB	U		U		U		

TABLE 4 continued.

Cedar waxwing *Bombycilla cedrorum*	T	U		U				
Loggerhead shrike *Lanius ludovicianus*	S				U	C		
European starling *Sturnus vulgaris*	PB	A	C	A		U	U	
Warbling vireo *Vireo gilvus*	S	R						
Yellow warbler *Dendroica petechia*	S	C		U				
Common yellowthroat *Geothlypis trichas*	S	C		U				
Yellow-breasted chat *Icteria virens*	SB	C	U	C	U	C		
Western tanager *Piranga ludoviciana*	M		R	R				
Black-headed grosbeak *Pheucticus melanocephalus*	S					R		
Blue grosbeak *Guiraca caerulea*	SB	U	C	C	U	C	U	
Lazuli bunting *Passerina amoena*	SB	C	U	C		U		
Indigo bunting *Passerina cyanea*	SB	U	U	C		U		
Rufous-sided towhee *Pipilo erythrophthalmus*	SB	C	C	C	U	A	C	
American tree sparrow *Spizella arborea*	W					U		
Brewer's sparrow *Spizella breweri*	M				U	U		
Clay-colored sparrow *Spizella pallida*	M				U	U		
Chipping sparrow *Spizella passerina*	SB		U	U	C	U		
Vesper sparrow *Pooecetes gramineus*	S				U	U		
Lark sparrow *Chondestes grammacus*	SB		U	C	U	C	U	
Lark bunting *Calamospiza melanocorys*	SB				C	U		
Grasshopper sparrow *Ammodramus savannarum*	SB				C			
White-crowned sparrow *Zonotrichia leucophrys*	M	C	C	C	U	C		C
Dark-eyed junco *Junco hyemalis*	W		C			C		
Red-winged blackbird *Agelaius phoeniceus*	S	C		U				
Western meadowlark *Sturnella neglecta*	SB		U	C	A	C		
Common grackle *Quiscalus quiscula*	SB	A		C		C		
Brown-headed cowbird *Molothrus ater*	SB	C		A	C	C		
Orchard oriole *Icterus spurius*	SB	U		C				
Northern oriole *Icterus galbula*	S	U		U	R			
House finch *Carpodacus mexicanus*	P	U		U		C		U
Pine siskin *Carduelis pinus*	P			U		U		
American goldfinch *Carduelis tristis*	PB	C	U	A	C	U	U	
House sparrow *Passer domesticus*	PB	C	U	C	U	C	U	

nest destruction. Of three nests located in June 1987, all had been destroyed following a severe hailstorm. The extent of pheasant nest predation was not determined. The greatest concentration of northern bobwhite (*Colinus virginianus*) was along the canal on the west side of SBNM where weedy plant species were abundant. Sightings of fledgings have documented the northern bobwhite's reproduction on adjacent lands, but no nests were located at SBNM.

GRUIFORMES AND CHARADRIIFORMES.—Species of these two orders were uncommon at SBNM (Table 4). In all three field seasons we observed a pair of upland sandpipers (*Bartramia longicauda*) in the prairie dog colony but found no nest. Herring gulls (*Larus argentatus*) and Franklin's gulls (*L. pipixcan*) were seen infrequently flying over SBNM between their feeding bouts in adjacent plowed fields in the spring.

COLUMBIFORMES AND CUCULIFORMES.—The mourning dove (*Zenaida macroura*), although not abundant, had nests located throughout SBNM. Five nests were located in 1987—three on the ground and two in trees. The only representative of the Cuculiformes order was the yellow-billed cuckoo (*Coccyzus americanus*), an uncommon summer resident in the riverine woodland.

STRIGIFORMES.—Great horned owls were common in the coniferous woodland and badlands. George Oviatt, SBNM resource manager, located a successful nest in a steep bank of the badlands in 1987. Other great horned owl nests were located in steep sandstone, clay banks. Two pairs of burrowing owls (*Athene cunicularia*) were sighted frequently in the prairie dog colony in 1986. In 1987, seven owls fledged from one clutch and five from another during the first week of July. Pellets collected on prairie dog mounds contained mostly prairie voles and various beetle species. The only barn owl (*Tyto alba*) seen was a road kill on 8 July 1987 along Highway 92.

CAPRIMULGIFORMES AND APODIFORMES.—We observed common poor-wills (*Phalaenoptilus nuttallii*) at dusk as they vocalized their distinctive call while flying over Scotts Bluff. Common nighthawks (*Chordeiles minor*) were observed over Scotts Bluff. The white-throated swift (*Aeronautes saxatalis*) was more abundant than the chimney swift (*Chaetura pelagica*), and nests of the former were located in crevices of Scotts Bluff. Also, fledglings were observed during August.

CORACIFORMES AND PICIFORMES.—Belted kingfishers (*Ceryle alcyon*) were commonly seen along the canal and shores of the Platte River. Although we located no nests, we suspected that the vertical bluffs in the river bottom provided potential nest sites. The northern flicker (*Colaptes auratus*) was the most abundant of the four woodpeckers at SBNM. Both red-shafted and yellow-shafted phases were observed, with SBNM located within their hybridization zone (NGS 1987).

PASSERIFORMES.—Four species of flycatchers were observed at SBNM (Table 4). The Say's phoebe (*Sayornis saya*), eastern kingbird (*Tyrannus tyrannus*), and western kingbird (*T. verticalis*) were found in the prairie dog colony, along the canal, and in mixed-grass prairie with shrub-dominated draws surrounding Scotts Bluff.

Barn swallows (*Hirundo rustica*), cliff swallows (*H. pyrrhonota*), and northern rough-winged swallows (*Stelgidopteryx serripennis*) were common along the canal, river, and their adjoining uplands. Large aggregations of cliff swallows foraged over the prairie dog colony and an adjacent western wheatgrass field.

The black-billed magpie (*Pica pica*) was the most abundant corvid. House wrens (*Troglodytes aedon*) were abundant in the canal riparian habitat and in the riverine woodland, while rock wrens (*Salpinctes obsoletus*) occupied slopes of bluffs, badlands, and shrub-dominated ravines.

Mountain (*Sialia currucoides*) and eastern bluebirds (*S. sialis*) were uncommon transients during spring and summer, whereas the Townsend's solitaire (*Myadestes townsendi*) was a common fall migrant in the coniferous woodlands. The American robin (*Turdus migratorius*) was widely distributed throughout SBNM, and brown thrashers (*Toxostoma rufum*) were found where there was abundant tree or shrub cover.

The introduced European starling (*Sturnus vulgaris*) had colonized the canal riparian habitat. It and the brown-headed cowbird (*Molothrus ater*) were the most abundant avian species along the canal. The only vireo species observed was the warbling vireo (*Vireo gilvus*) in the riverine woodland.

Three wood warbler species were present at SBNM (Table 4). The yellow warbler

(*Dendroica petechia*) and common yellowthroat (*Geothlypis trichas*) were seen in the canal riparian and riverine woodland habitats. Yellow-breasted chats (*Icteria virens*), found in these two habitats, were also common in shrub-dominated slopes and in the coniferous woodland.

The black-headed grosbeak (*Pheucticus melanocephalus*) was infrequent in the shrub-dominated slopes. Blue grosbeaks (*Guiraca caerulea*) were abundant in thickets along the canal and in shrub-dominated slopes. Both the lazuli bunting (*Passerina amoena*) and indigo bunting (*P. cyanea*) were common within the same habitats as the blue grosbeak.

Rufous-sided towhees (*Pipilo erythrophthalmus*) were conspicuously abundant at SBNM. They nested in thick vegetation of shrubs and vines and, like the robin, occurred in almost every habitat type at SBNM.

Ten species of sparrows occurred at SBNM (Table 4). Lark buntings (*Calamospiza melanocorys*), lark sparrows (*Chondestes grammacus*), chipping sparrows (*Spizella passerina*), and grasshopper sparrows (*Ammodramus savannarum*) all bred at SBNM. Lark sparrows utilized juniper stands for nest sites, whereas chipping sparrows nested in and around deciduous trees along the canal. The other summer resident, the vesper sparrow (*Pooecetes gramineus*), was uncommon in the grasslands north and west of Scotts Bluff. Large migratory flocks of white-crowned sparrows (*Zonotrichia leucophrys*) were present in the fall and spring. Migrating Brewer's sparrows (*Spizella breweri*) and clay-colored sparrows (*Spizella pallida*) were observed in the trees surrounding the headquarters in May 1988.

The red-winged blackbird (*Agelaius phoeniceus*), the only blackbird at SBNM, was seen exclusively in the canal riparian habitat and the riverine woodland. Western meadowlarks (*Sturnella neglecta*) were prominent throughout the mixed-grass prairie.

Common grackles (*Quiscalus quiscula*) were abundant in the prairie dog colony and common wherever trees were located; most nests were found in cottonwood and willow trees along the canal. The brown-headed cowbird was the most abundant bird on the line transects within the canal riparian habitat.

Orchard orioles (*Icterus spurius*) were more abundant than the bullock's race of the northern oriole (*I. galbula*) at SBNM. Orchard orioles were concentrated along the canal and in the riverine woodland. Northern orioles were found in both deciduous tree stands and adjacent grasslands.

American goldfinches (*Carduelis tristis*) were abundant throughout SBNM, with highest densities along the canal. House finches (*Carpodacus mexicanus*) were associated with shrubby vegetation within riparian areas, grasslands, and the badlands. Both house finches and pine siskins (*Carduelis pinus*) were permanent residents. The house sparrow (*Passer domesticus*), another introduced North American species, was common around the visitor center and canal riparian habitat.

The canal riparian habitat transect had significantly greater overall bird abundance (41 birds/100 ha ± 7.39) compared with the two transects in mixed-grass prairie and shrub-dominated slopes ($F = 15.15$, $P < .001$). Species richness was also greatest in the canal riparian habitat transect (22 ± 4.09) compared with the other two transects ($F = 4.79$, $P < .100$). The Shannon diversity index for the canal riparian habitat transect was not significantly different from the other two transects ($F = 1.98$, $P = .100$).

Mammals

MARSUPIALIA AND INSECTIVORA.—Opussums (*Didelphis virginiana*) were observed along the irrigation canal east and west of SBNM, and tracks were found along the canal within SBNM boundaries (Table 5). The eastern mole (*Scalopus aquaticus*) was the only species of this order found at SBNM. The prairie dog colony, side slopes of draws, and disturbed grassland sites had the highest densities.

CHIROPTERA.—The only bats observed were the small-footed myotis (*Myotis liebii*) and big brown bat (*Eptesicus fuscus*). The small-footed myotis was the most common bat captured in the tunnels of the summit road. Small-footed myotis were also sighted feeding over the canal.

LAGOMORPHA.—Desert cottontails (*Sylvilagus audobonii*) were found in the more xeric areas such as the bluffs, grasslands, and shrub-dominated slopes. Small shrubs, like snowberry and skunkbush sumac, were used by desert cottontails for cover and feeding sites within grasslands and associated gullies.

TABLE 5. Mammalian species residency status, distribution by habitat, and relative abundance at Scotts Bluff National Monument. Abbreviations are explained in Table 1.

		Habitat types						
Common name *Scientific name*	Residency status	RW	CW	CRH	MGP	S	PSB	B
Virginia opossum *Didelphis virginiana*	P	R		U				
Eastern mole *Scalopus aquaticus*	PB	C	U	U	C			
Small-footed myotis *Myotis leibii*	SB	C		C			A	
Big brown bat *Eptesicus fuscus*	SB						U	
Desert cottontail *Sylvilagus audubonii*	PB		U		A	C	C	U
Eastern cottontail *Sylvilagus floridanus*	PB	C	U	C	C	C		
Black-tailed prairie dog *Cynomys ludovicianus*	PB				C			
Fox squirrel *Sciurus niger*	PB	U		U				
Plains pocket gopher *Geomys bursarius*	PB	C	U	U	A	U		
Hispid pocket mouse *Perognathus hispidus*	PB				C			
Ord's kangaroo rat *Dipodomys ordii*	PB				U			
Western harvest mouse *Reithrodontomys megalotis*	PB				C		U	
Deer mouse *Peromyscus maniculatus*	PB	C	C	C	A	C	C	U
Bushy-tailed woodrat *Neotoma cinerea*	P						U	
House mouse *Mus musculus*	PB				C			
Prairie vole *Microtus ochrogaster*	PB	C		C	A	U		U
Meadow vole *Microtus pennsylvanicus*	PB	C						
Muskrat *Ondatra zibethicus*	T			U				
Porcupine *Erethizon dorsatum*	P		U					
Coyote *Canis latrans*	PB		U	U	C	C	U	
Red fox *Vulpes vulpes*	P	U		R	U			
Raccoon *Procyon lotor*	P	U		C	U		U	
Long-tailed weasel *Mustela frenata*	P	U			U	U		
Mink *Mustela vison*	P			U				
Badger *Taxidea taxus*	T				R			
Striped skunk *Mephitis mephitis*	P	U		U				
Mule deer *Odocoileus hemionus*	PB	U	C	U	C	A	U	U
White-tailed deer *Odocoileus virginianus*	PB	C		U	U	U		

Eastern cottontails (*S. floridanus*) inhabited wooded, more mesic sites but also were found in the grasslands in association with desert cottontails. Both the white-tailed jackrabbit (*Lepus townsendii*) and the black-tailed jackrabbit (*L. californicus*) were absent from SBNM; their extirpation from the park was further substantiated from interviews with ranchers in adjacent areas.

RODENTIA.—Two sciurids occurred at SBNM, the fox squirrel (*Sciurus niger*) and the black-tailed prairie dog. In 1986 two adjoining prairie dog colonies existed in the extreme northwestern corner of SBNM near the irrigation canal; the prairie dogs were discovered at SBNM in 1982, after having been absent since 1941 (Franklin 1983). In 1986 both colonies were censused by live-trapping all individuals—109 in the old colony nearest the canal and 89 in the new colony directly south of the old one. Both colonies combined occupied 5.77 ha in August 1986. In spring 1987, after pup emergence, the old colony had 213 prairie dogs and the new colony 88. Both colonies combined occupied 8.63 ha in August 1987 (1.1% of SBNM's inhabitable grassland). We found a number of animals coexisting with the prairie dogs within this microhabitat, including Woodhouse's toads, prairie rattlesnakes, western box turtles, prairie voles, hispid pocket mice (*Perognathus hispidus*), Ord's kangaroo rat (*Dipodomys ordii*), cottontail rabbits, burrowing owls, upland sandpipers, lark buntings, and kingbirds. The fox squirrel occurred at SBNM in the riverine woodland and canal riparian habitat in low numbers.

Plains pocket gophers (*Geomys bursarius*) were abundant in the grasslands throughout SBNM. Pocket gopher densities were estimated by counting fresh gopher mounds (Reid et al. 1966). With a sampling estimate of 25 mounds/ha, pocket gopher densities were estimated at 4.67/ha within mixed-grass prairie (see Vaughan 1961).

Localized populations of hispid pocket mice occurred in disturbed mixed-grass prairie containing a variety of exotic broadleaf plant species and a large volume of seeds resulting from previous dry land farming. Despite 4,150 trap nights from 6 June to 15 August 1986 and 4 April to 14 June 1987 throughout the entire SBNM, Ord's kangaroo rats were captured only within the prairie dog colony.

Western harvest mice (*Reithrodontomys megalotis*) occurred in the prairie dog colony and other grassland sites. Deer mice (*Peromyscus maniculatus*) were the most widely distributed small mammal at SBNM, as they are in many other regions of the United States. They were captured in all types of grassland sites, ravines, riverine woodland, and on top of Scotts Bluff. Population estimates for deer mice were calculated using the program CAPTURE (Otis et al. 1978). Naive density estimates (calculated by dividing the estimated population size by a naive estimate of the area trapped) from removal trapping at a site predominantly covered by kochia, previously occupied by a feedlot, and on top of Scotts Bluff were 31.5 deer mice/ha and 12.5 deer mice/ha, respectively. The naive density estimate from mark-recapture sampling in a sparsely vegetated area along the base of South Bluff was 11.9 deer mice/ha.

Bushy-tailed woodrats (*Neotoma cinerea*) were uncommon at SBNM. They have been found almost exclusively in rocky areas, with their houses situated in crevices and cracks beneath rocks and occasionally in man-made structures (Jones et al. 1983).

The house mouse (*Mus musculus*), an introduced Eurasian species, occurred in and amongst storage buildings and in exotic broadleaf vegetation sites, such as the old feedlot next to the prairie dog colony. The *Mus* population was sampled along the same transect as the *Peromyscus* population, next to the prairie dog colony. Naive density was estimated to be a minimum of 31.5 house mice/ha—*Mus* trapping success never decreased during the four-day sampling period.

Both prairie voles and meadow voles (*Microtus pennsylvanicus*) occurred at SBNM. The prairie vole, the most abundant small mammal in the grassland habitat, also inhabited the badlands, riverine woodland, canal riparian habitat, and rocky areas. Program TRANSECT was used to estimate vole densities in the trapping web (Anderson et al. 1983). Prairie vole density for the late-April trapping session in 1987 was 38.54 voles/ha (S.E. ± 14.16).

Muskrats (*Ondatra zibethicus*) occurred mostly as transients along the canal. The North Platte River does not flood far enough inland to create standing water at a level for muskrat dens to be constructed; thus, muskrat shelter was limited to dens burrowed in the riverbank.

The porcupine (*Erethizon dorsatum*) was found in the coniferous woodland in all seasons and in adjacent prairie during the spring, summer, and fall. Pine tree girdling was evident but not excessive in the coniferous woodland and slopes of South Bluff. The entire population of porcupines at SBNM was estimated to be less than 10.

Carnivora.—In July 1986 three coyote (*Canis latrans*) pups were observed in draws west of Scotts Bluff. On 7 August 1987 four juvenile coyotes and an adult were observed foraging at the northwestern base of Scotts Bluff. Coyote scats were found throughout the prairie dog colony; these contained remains of prairie voles, but not of prairie dogs. The coyote population in August 1987 was estimated to be 10–20 individuals. Red fox (*Vulpes vulpes*) tracks were encountered occasionally along the canal. Our only sighting of a red fox was in a drainage next to the riverine woodland. In 1985 a red fox was chased from the top of Scotts Bluff and over a cliff by a domestic dog.

Raccoons (*Procyon lotor*) occurred in the canal riparian habitat, river woodland, areas of dense cover, and water drainages. Estimates based on tracks and observations indicated that SBNM's raccoon population was 5–20 individuals.

A long-tailed weasel (*Mustela frenata*) skull was found along the southwest boundary fence in 1987. In June 1988 a long-tailed weasel was captured during our live-trapping of prairie dogs. The weasel was possibly using an abandoned prairie dog burrow as a den site. In June 1988 a mink (*Mustela vison*) was observed along the canal bank on the east side of the SBNM. A three-quarter grown badger was sighted by a park employee in a snowberry thicket directly north of the visitor center in July 1987. In April 1988 we found 36 prairie dog burrow mounds in the new colony that had been dug out by a badger. Striped skunks (*Mephitis mephitis*) were observed during spotlighting along the canal and adjacent lands in 1987. Tracks also were found within the river woodland. Insufficient information was available to estimate their numbers.

Artiodactyla.—Both mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) occurred at SBNM. Mule deer used all habitat types. In the spring and summer, they tended to graze more on grasses and forbs than to browse on trees and shrubs. Sightings of white-tailed deer were mostly restricted to the riverine woodland and mixed-grass prairie north of Scotts Bluff. We suspect that hybridization occurs at SBNM. A male deer having a distinct white-tailed antler formation but with a black tail was observed next to the canal during the summer of 1986.

Recruitment by the deer population indicated a growing and healthy population. In 1987 fawns were observed throughout the entire fawning period. Ten different mule and three different white-tailed deer fawns were detected. Because SBNM is small and deer movement across its boundaries is common (especially during the winter), large variations in population estimations were observed. In broad terms, the 1987 population was estimated to be between 50 and 100 individuals (86% mule deer, based on daily records of deer species throughout the study).

Species Richness by Habitat

Figure 2 shows the distribution of species by habitat type. The riverine woodland, which accounts for only 4% of the total area, had 57% of the total species. The canal riparian habitat, which makes up 6% of the area, had 54% of the total species. The mixed-grass prairie's surface area of 47% was proportional to its 50% species occurrence. The riverine woodland and canal riparian habitat had the greatest percentage of bird species at 58% and 54%, respectively. The richest mammalian habitat was the mixed-grass prairie, with 71% of the total mammalian species. The herpetofauna species richness was greatest in the riverine woodland. Fourteen wildlife species were unique in the riverine woodland and 12 in the mixed-grass prairie.

Potentially Present Species

Of the possible 234 wildlife species recorded in the local vicinity of SBNM, only 136, or 58% were found to occur at SBNM. Herpetofauna cited by Lynch (1985) as occurring in Scotts Bluff County but not observed during the survey were: northern leopard frog (*Rana pipiens*), bullfrog (*Rana catesbeiana*), short-horned lizard (*Phrynosoma

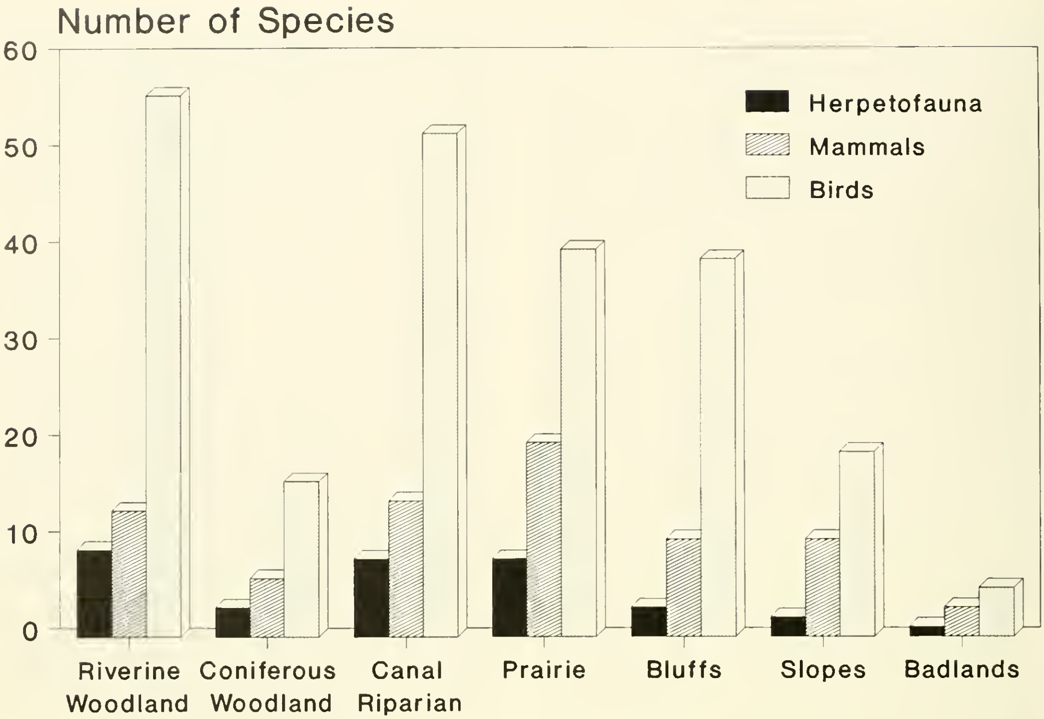

Fig. 2. Wildlife species richness for seven habitat types at Scotts Bluff National Monument.

douglassii), lesser earless lizard (*Holbrookia maculata*), northern prairie lizard (*Sceloporus undulatus*), western hognose snake (*Heterodon nasicus*), and milk snake (*Lampropeltis triangulum*).

Numerous avian species cited by observers in Nebraska Bird Review since 1985 and Johnsgard (1979) as occurring or breeding in the Nebraska Panhandle were not observed during this study. These included: 1 species of loon, 3 grebes, 1 pelican, 4 herons and bitterns, 14 waterfowl species, 4 raptors, 1 crane, 19 shorebirds, 1 cuckoo, 3 owls, 2 hummingbirds, 1 woodpecker, and 20 passerines.

Mammalian species cited by Jones et al. (1983) and Jones and Choate (1978) as occurring in the Panhandle but not found during the survey were: masked shrew (*Sorex cinereus*), silver-haired bat (*Lasionycteris noctivagans*), red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), fringed-tailed myotis (*Myotis thysanodes*) (all bat species are seasonal migrants), black-tailed jackrabbit, white-tailed jackrabbit, northern pocket gopher (*Thomomys talpoides*), olive-backed pocket mouse (*Perognathus fasciatus*), plains pocket mouse (*Perognathus flavescens*), silky pocket mouse (*Perognathus flavus*), plains harvest mouse (*Reithrodontomys montanus*) northern grasshopper mouse (*Onychomys leucogaster*), spotted ground squirrel (*Spermophilus spilosoma*), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), beaver (*Castor canadensis*), bobcat (*Felis rufus*), and gray fox (*Urocyon cinereoargenteus*). Future work at SBNM may find some of these species to be present.

DISCUSSION

The relatively low wildlife species richness compared to the potential species richness at SBNM was due to either species absence or species presence in low densities difficult to detect. Species presence in low densities can be attributed to the limited area of SBNM. Species absence was mainly due to the lack of sandy-soil blowouts, indicative of sandhill prairies, and wetland complexes. Absence was due also to the limited area of the existing habitat types and possibly to land practices and human activity adjacent to SBNM. One could describe the Monument as an insular park (Buechner 1985), surrounded by agricultural land.

No species was exceedingly abundant in any habitat, but a few were quite rare in various habitats. Species distribution was in three major habitats—riverine woodlands, canal riparian habitat, and mixed-grass prairie. The riverine woodland was the major habitat type providing avian diversity at SBNM. Anderson et al. (1987) found that moist habitats of riparian and wetland areas had the greatest species richness and diversity. Even though the man-created canal riparian habitat along the irrigation canal was only 6% of the SBNM area, avian species richness and abundance was greater there than in the native prairie or shrub-dominated slopes.

The low species richness of amphibian life at SBNM probably is normal for a vicinity that lacks shallow water basins and is typified by low annual precipitation. Efforts should be made to preserve small drainages leading into the river and shallow water basins and prevent any disturbance during the spring and summer. Though the prairie rattlesnake was abundant throughout the mixed-grass prairie, its densities are not thought to be in excess. With exceptions of isolated populations of house mice, the prairie vole may be the major prey species for rattlesnakes at SBNM. In addition, it seemed that bullsnakes were in association with abundant house mice populations. Bullsnakes have been reported by other investigators (Hammerson 1982) in areas of locally abundant small mammal populations.

A black-footed ferret (*Mustela nigripes*) reintroduction would not be feasible at SBNM because of the extremely small prairie dog population. The present prairie dog population size of approximately 250 individuals is far below the recommended population of 766 prairie dogs required to support one black-footed ferret (Fagerstone and Biggins 1986). Both the prairie dog and the pocket gopher were found to provide microhabitat for other wildlife species at SBNM during our study. Agnew et al. (1986) found similar wildlife species to be abundant on prairie dog colonies in western South Dakota. The pocket gopher, a fossorial mammal like the prairie dog, has the potential to locally impact the native plant species composition on SBNM's native prairie. Though pocket gophers have been found to reduce forage production on rangeland sites primarily for cattle grazing (Foster and Stubbendieck 1980), SBNM is not a rangeland for cattle nor is forage production a major concern at this time. Pocket gopher mounds function in providing shelter for a variety of amphibians, reptiles, and small mammals (see Vaughan 1961), a vital link in the grassland ecosytem.

The occurrence of kangaroo rats only in the prairie dog colony was probably because of their selection of seeds from the weedy plant species associated with the colony and abandoned burrow sites. Meserve (1971) calculated densities of 10–14 prairie voles/acre (25–35/ha) at SBNM, slightly lower than our estimates. This could be interpreted as little change having occurred since 1971 in the litter depth and plant species of the prairie.

Red fox numbers may be regulated by the coyote population through interspecific competition (Major and Sherburne 1987), but the low numbers also may have been because of the preference of red foxes for more riparian habitats and wooded areas (Jones et al. 1983). The SBNM raccoon population may be quite mobile and cover large distances along drainages in search of easily accessible food sources such as the garbage dumpster sites at SBNM. Densities have been reported to range from 0.5/km^2 on the prairies of North Dakota (Fritzell 1978) to 20/km^2 in bottomlands and marshes of Alabama (Johnson 1970).

With an increase in wooded riparian habitat and agricultural practices and a reduction of rangeland, white-tailed deer populations have increased in the Nebraska Panhandle in recent years (Menzel 1984). Little is known about the interaction of sympatric populations of mule and white-tailed deer. Though they are considered two separate species, hybridization has been documented in Texas, Kansas, Nebraska, Washington, and Alberta (Stubblefield et al. 1986, Day 1980, Wishart 1980, Kramer 1973). Wishart (1980), studying a captive herd in Alberta, found that some hybrids were fertile and produced viable offspring.

Though SBNM is relatively small, there is the potential for the National Park Service to reintroduce absent native wildlife species. We believe that with cooperation and support from adjacent landowners and local citizens, pronghorn antelope (*Antilocapra americana*) and the sharp-tailed grouse (*Tympanuchus phasianellus*) are two possible candidates for reintroduction. SBNM's small size of 1,200 ha is an important factor in determining whether it would accommodate the average home range size of pronghorn. Home ranges have been found to vary from 440 to more than 1,200 ha for nursery and bachelor herds in Palouse Prairie habitat (Kitchen 1974), averaging 1,385 ha for male and females in Idaho (Reynolds 1984), and ranging from 165 to 2,300 ha in central Montana (Bayless 1969). We believe pronghorn could greatly enhance the existing fauna, but the decision must be made on the basis of a thorough evaluation of SBNM's food base and the potential impact on surrounding private lands.

Booming grounds for breeding purposes are an important part of the sharp-tailed grouse life cycle. Booming grounds are established year after year in areas of bare or grassy knolls (Swenson 1985). Male grouse often show preferential use of arenas burned by fire (Sexton and Gillespie 1970). If grouse were reintroduced to SBNM, a small, elevated area of prairie should be burned the first year they are transplanted to entice males to set up booming grounds on the burn site.

ACKNOWLEDGMENTS

We thank Erwin E. Klaas, Paul A. Vohs, and J. Knox Jones, Jr., for their review of the manuscript; we also appreciate the cooperation of SBNM's staff and the field assistance from Jack Holloway III, Dwaine Hurt, Lynne Vacanti, and Scot Schliecher. Funding was provided by the National Park Service through an interagency cooperative agreement, IA-6000-6-8005, with the Fish and Wildlife Service, Cooperative Research Unit Center, Region 8, Iowa Cooperative Fish and Wildlife Research Unit.

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RESPONSE OF NESTING WATERFOWL TO FLOODING IN GREAT SALT LAKE WETLANDS

A. Lee Foote[1]

ABSTRACT.—Great Salt Lake wetlands were inundated in 1983, displacing approximately 20,000 nesting waterfowl. Ten protected marshes in the Great Basin were surveyed for changes in numbers of breeding pairs of waterfowl during each of four years preceding Great Salt Lake flooding and four years following flooding. The hypothesized increase in numbers of breeding birds did not occur, indicating that flood-displaced waterfowl did not move into nearby suitable habitat to nest.

Much research has addressed waterfowl response to region-wide drought conditions (Hansen and McKnight 1964, Smith 1970, Henny 1973); yet little is known about waterfowl response to more localized flooding. This paper investigates changes in regional breeding populations of three species of ducks prior to and following extensive flooding of Great Salt Lake shoreline marshes.

The marshes along the north and east shores of Great Salt Lake have been extremely important breeding grounds for redheads (*Aythya americana*) (Weller 1964) and cinnamon teal (*Anas cyanoptera*) (Bellrose 1976). Gadwalls (*Anas strepera*) and mallards (*Anas platyrhynchos*) were also locally common breeders (Williams and Marshall 1938).

Continental subpopulations such as these operate under a migratory tradition; after maturing, females return to the marsh near the area in which they were raised.

Hens that nest successfully in a given wetland show strong tendencies to return to the same part of the same wetland year after year (Borden and Hochbaum 1966, Doty and Lee 1974, Bishop et al. 1978). This behavior is called philopatry and, in an evolutionary perspective, may have strong selective advantages. Relinquishing philopatry and seeking suitable alternative habitats in response to drought is essential (Weller 1964). This also raises the question of whether or not waterfowl have some instinctive contingency response when they return or "home" to previously used marshes and find them unsuitable. Pintails (*Anas acuta*) homing to drought-stricken prairie potholes have been shown to overfly to the more stable wetlands in Alaska and Siberia, USSR (Henny 1973, Derkson and Eldridge 1980). Redheads may respond similarly but not travel as far north (Weller 1964). Blue-winged teal (*Anas discors*) may move north and west, and lesser scaup (*Aythya affinis*) appeared to shift eastward from drought-stricken Saskatchewan (Rogers 1959). In each of these cases ducks have moved out of a large area of lowered habitat quality. Their response may be quite different when faced with flooding of a much smaller, yet intensively used area of breeding habitat such as Great Salt Lake marshes.

During 1983–1986 the Great Salt Lake experienced consecutive record-breaking lake level rises, inundating approximately 175,000 ha of wetlands. Shorelines and emergent stands of plants were completely overtopped with as much as 3 m of water; in addition, wind-induced seiches caused wave-wash into areas up to .75 m above this extreme lake level. Essentially all 175,000 ha of Great Salt Lake nesting habitat had been temporarily eliminated.

From previous studies (Williams and Marshall 1938, Bellrose 1976, Utah Division of Wildlife Resources, unpublished data) I estimate that over 20,000 ducks nested in the Great Salt Lake marshes prior to flooding. The number of individual birds, returning adults and offspring of the previous year's birds, homing to these marshes cannot be estimated directly. However, Doty and Lee (1974) found that 46% of female mallards returned to previously used nest sites (baskets in this study), and virtually all successful females that survived returned to nest within 10 km of the previous year's nest. It seems reasonable to expect that perhaps 10,000–15,000 pairs (young of the previous season and 2+-year-old females) would return to their previously used marshes. Fifteen thousand nesting pairs of returning birds represents approximately one third of Utah's total waterfowl nests.

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Utah is the second driest state in the United States, and the wetlands that occur here are usually discrete units of quality habitat in a desert setting. Many of these wetlands are government-owned and managed for waterfowl habitat. I refer to these wetland "islands" of quality habitat in a desert region as "satellite marshes."

Bancroft et al. (1988) documented colony relocations by wading birds in consecutive years resulting from hydrological changes. When Great Salt Lake flooded the stands of emergent vegetation in the adjacent shoreline marshes, several large colonies of Franklin gulls (*Larus pipixcan*) and white-faced ibis (*Plegadis chihi*) moved to nearby satellite marshes to nest. This raised the question of whether waterfowl that returned to nest in the flooded marshes might have displaced into nearby suitable habitat as well.

METHODS

The objective of this study was to see if these, the best available data, indicate a displacement of nesting waterfowl from the Great Salt Lake marshes into nearby suitable habitats such as satellite marshes. Spring pair counts were used to estimate changes in duck numbers on satellite marshes coincident with bird displacement from Great Salt Lake marshes.

The hypothesis is that if displaced ducks nested in satellite marshes, an increase in breeding pairs would be observed there after Great Salt Lake flooding occurred.

The study period was 1979–1986, four years of data from the preflooding period and four years postflooding. For study areas 10 satellite marshes were selected that fit the following criteria:

1. All were within 100 km of Great Salt Lake.
2. Each presented suitable nesting habitat for the entire study period.

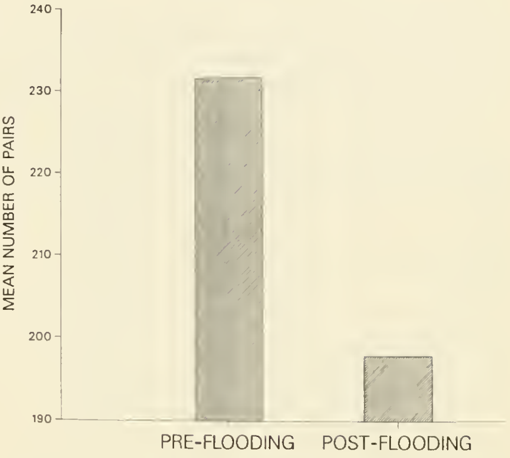

Fig. 1. Mean numbers of indicated breeding pairs of cinnamon teal, gadwalls, and redheads on 10 marshes for the four years before and the four years after the Great Salt Lake flooded.

3. Spring pair count data were available for each marsh throughout the study period.

I requested and received from the Utah Division of Wildlife Resources spring pair count data for the 1979–1986 period on gadwall, cinnamon teal, and redhead, the three most common species of nesting ducks in the Great Salt Lake marshes.

The explicit assumptions of this investigation were:

1. That territorial space was available on the satellite areas and that ducks would distribute themselves in the manner of an "ideal free distribution" (Fretwell and Lucas 1970).
2. That satellite areas chosen were a representative sample of Great Basin wetlands.

Pair data were analyzed with a three-way analysis of variance (year/flood × marsh × species) to detect differences between factors and between combinations of factors.

RESULTS AND DISCUSSION

There was not a significant difference ($P = .254$) in pair numbers counted on satellite marshes during the four preflood years and the four postflood years (Fig. 1). From this it was concluded that there was not an increase in pair numbers on satellite marshes coincident with the flooding of Great Salt Lake marshes.

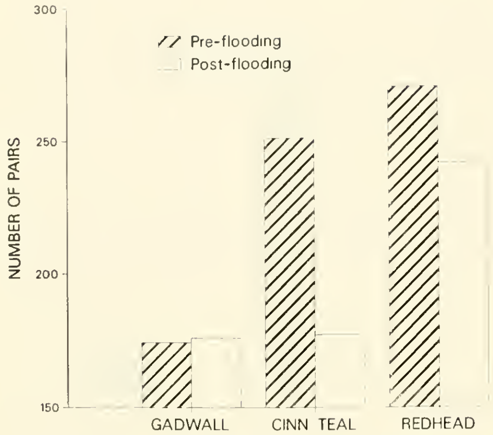

Fig. 2. Mean numbers of indicated breeding pairs of cinnamon teal, gadwalls, and redheads on 10 marshes for each survey year.

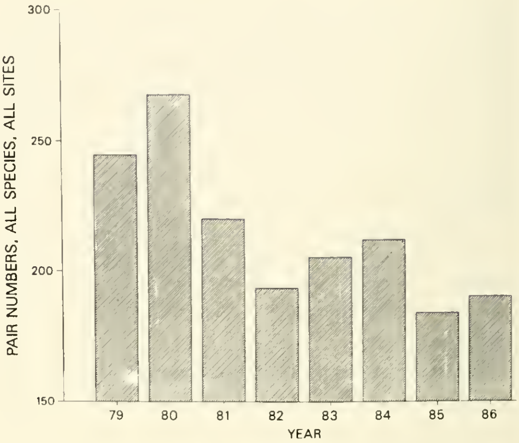

Fig. 3. Mean numbers of indicated breeding pairs of three species of ducks on 10 marshes before and after flooding of Great Salt Lake.

The year/flooding interaction reflected a general and significant decrease (P = .319) in numbers with time (Fig. 2). The magnitude of decrease correlated well (r = .76) with the decreases in continental breeding populations reported by the U.S. Fish and Wildlife Service (1988).

The refuge × species × flood interaction was significant; for this reason Fisher's least significant difference test was used to find which combinations were significant. Only four combinations were both logical comparisons and significant, and in each case the numbers changed in the downward direction.

Because band data for spring migrants is so scant, most duck movement information is anecdotal, or, as in the case of this study, inferred from relative changes in numbers coincident with discrete events or years. Hard data are not available; therefore, this study attempted to use available descriptive data, general trends, and logic to infer waterfowl movements.

As mentioned earlier, pintails have been shown to assess previously used wetlands as unsuitable, and then continue moving northward out of the region. Although exact settling locations (Johnson 1978) are unknown for displaced ducks, I suspect that ducks continued on past the flooded Great Salt Lake marshes, as do the bulk of the spring migrants. Pre- and postflood numbers of pairs were compared after sorting by species (Fig. 3). Gadwalls changed little, but cinnamon teal and redhead numbers decreased greatly. Cinnamon teal appear to have responded by moving out of the area. In 1983, concurrent with Great Salt Lake flooding, Canadian Wildlife Service biologists noted unprecedented numbers of cinnamon teal in British Columbia where they are usually uncommon. This probably resulted from long-distance immigration.

It is concluded that waterfowl numbers did not increase significantly on satellite marshes following flooding of the Great Salt Lake marshes; therefore, I reject my hypothesis of local displacement. Given that habitat for 20,000 duck pairs was removed in one season, that ducks are philopatric, and that satellite breeding populations did not increase, it appears that most nesting ducks moved out of the Great Salt Lake region to find suitable nesting habitat elsewhere.

ACKNOWLEDGMENTS

The author thanks T. Aldrich and J. Huener, Utah Department of Natural Resources, for critical review of the concepts in this paper. The Ecology Center at Utah State University provided financial support for this study.

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NOTE ON FUNGI IN SMALL MAMMALS FROM THE *NOTHOFAGUS* FOREST IN ARGENTINA

Javier G. Perez Calvo[1], Zane Maser[2], and Chris Maser[3]

ABSTRACT.—Fungal spores from the same taxa of fungi that occur in the Pacific Northwest are reported from digestive tracts of 31 rodents of 5 genera from the *Nothofagus* forest of southern Argentina. Mycophagy (fungal feeding) by forest rodents has been well documented in North America (Fogel and Trappe 1978, Maser et al. 1978, McIntire 1984, and others), Europe (Blaschke and Bäumler 1986, Durrieu et al. 1984), and Australia (Malajczuk et al. 1987). The purpose of this note is to report fungi consumed by rodents of the Argentine Andinian Patagonic forest (see Dimitri 1972, McQueen 1977, and Ward 1965 for a discussion of this forest), where mycorrhizal fungi may be an important part of the forest-rodent ecology (Cabrera and Yepes 1960, Pearson 1983, 1948, Pearson and Pearson 1982).

Thirty-one individuals of five genera of rodents were captured at Cerro Otto, 5 km (8 mi) west of San Carlos de Bariloche, Provincia Río Negro. The habitat is a stand of lenga (*Nothofagus pumilio*), a beechlike tree, with two distinct understories: (1) pure, dense bamboo (*Chusquae coleou*) and (2) mixed amancay (*Alstroemeria aurantiaca*), laura (*Schinus patagonicus*), *Berberis serratodentata*, and a few scattered bamboo. The study area represents the ecotone between the Argentine Andinian Patagonic forest and the Patagonic steppe.

Four species of rodents (*Akodon longipilis*, *Auliscomys micropus*, *Chelemys macronyx*, and *Oryzomys longicaudatus*) were caught in snap traps, and the fossorial rodent *Ctenomys haigi* was caught in Macabee[4] traps. The rodents were trapped from the beginning of March to the end of May in both 1983 and 1984. Voucher specimens, prepared by using standard museum techniques, are in the possession of the senior author.

Digestive tracts were preserved in 10% formalin, and their contents were examined at 100X, 400X, and 1,000X magnification. A small amount of equally mixed material was randomly sampled from each vial with narrow, parallel-sided forceps, placed on a microscope slide, wetted with a drop of Melzer's reagent (I, KI, and chloral hydrate), and enclosed under a 22 × 40 mm cover slip. The slide was systematically examined for fungal spores. Fungal taxa were identified with the aid of a spore key (Castellano et al., in press) and consultations with J. M. Trappe. We used percentage of frequency of fungi eaten to gain some idea of the propensity with which the rodents ate fungi.

RESULTS AND DISCUSSION

Twenty-three taxa of fungi were identified (Table 1).

Akodon longipilis (South American field mouse).—Although *A. longipilis* is normally considered to be omnivorous, consuming a high proportion of insects and their larvae, our study shows fungi of 18 taxa in its digestive tract (Table 1).

Auliscomys micropus (no English name).—This species is characterized as nearly exclusively herbivorous, but we found it to have eaten fungi of nine taxa (Table 1).

Chelemys macronyx (no English name).—Although this rodent is largely fossorial, particularly under the cover of snow, it is also active on the surface of the ground and ingested at least parts of fungi of 15 taxa (Table 1).

Oryzomys longicaudatus (long-tailed rice rat).—This rice rat is considered to be primarily granivorous (Meserve and Glanz 1978, Murúa et al. 1980), but we found it to have eaten fungi representing five taxa (Table 1).

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TABLE 1. The occurrence of fungal taxa from 29 rodents of 4 genera in Argentina, as indicated by examination of contents of digestive tracts. The two specimens of *Ctenomys haigi* have been omitted from this table because they contained no fungi.

Fungal genera	*Akodon longipilis* (N = 13)	*Auliscomys micropus* (N = 6)	*Chelemys macronyx* (N = 7)	*Oryzomys longicaudatus* (N = 3)
ASCOMYCETES				
Hypogeous				
Elaphomyces spp.	—	—	2	—
Genea spp.	—	—	1	—
G. fragilis	—	—	1	—
Unidentified	1	1	2	—
BASIDIOMYCETES				
Hypogeous				
Gautieria spp.	4	1	1	—
Hymenogaster spp.	7	4	1	—
Hysterangium spp.	10	3	6	—
H. purpurea	2	—	—	—
Melanogaster spp.	3	—	—	—
M. tuberiformis	1	—	—	—
Octavianina spp.	2	—	—	—
Pachyphloeus spp.	1	—	—	—
Radiigera spp. or *Sclerogaster* spp.	3	—	—	—
Rhizopogon spp.	—	1	1	—
Stephensia spp.	1	—	—	—
Unidentified	2	3	1	—
ZYGOMYCETES				
Hypogeous				
Glomus spp.	3	—	2	1
G. australe	3	—	1	—
G. fuegiana	1	—	1	—
G. macrocarpum	—	—	—	1
EPIGEOUS				
Bolbitiaceae	3	3	2	2
Boletacea	7	5	4	2
Certinareacea	8	5	5	1
Unidentified	4	1	—	1
TOTAL	66	27	31	8

Ctenomys haigi (no English name).—This fossorial rodent was trapped in an opening in the forest known locally as "pampita," a place where a now nonexistent village once stood. Although this rodent is not considered a forest dweller in the strict sense (Pearson 1984), the animal's burrows were found to penetrate the forest and so it is included in our study. It is of interest that the two *C. haigi* examined contained no fungi (Table 1), although its North American analogue *Thomomys* is known to eat both Basidiomycetes and Ascomycetes (Maser et al. 1978, 1988).

CONCLUSION

Even with our admittedly small sample of rodents and tiny sample of fungi from the *Nothofagus* forest of Argentina, all but one of the genera of hypogeous fungi identified from the rodents' intestinal tracts occur in the Pacific Northwest. The one genus, *Pachyphloeus* spp., not occurring in the Pacific Northwest occurs in central California. There seems to be some possibility for the occurrence of symbiotic relationships between forest rodents and forest vegetation in Argentina similar to those that occur between forest rodents and forest vegetation in North America. Further study is required to better understand the interdependency of rodents, fungi, and mycorrhizal host plants in Argentina.

ACKNOWLEDGMENTS

Efrén Cazares helped with the identifications of the fungi. Donald K. Grayson (Burke Museum of Natural History, University of

Washington, Seattle), Randy Molina (USDA Forest Service, Forestry Sciences Laboratory, Corvallis, Oregon), and John O. Whitaker, Jr. (Department of Life Sciences, Indiana State University, Terre Haute, Indiana) critically read and improved this paper. We sincerely appreciate their help.

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NOTE ON MOUND ARCHITECTURE OF THE BLACK-TAILED PRAIRIE DOG

Richard P. Cincotta[1]

ABSTRACT.—The development of black-tailed prairie dog (*Cynomys ludovicianus*) burrow mounds was monitored for three years. Entrances were flagged at points where a prairie dog was observed digging into the ground (primary entrances, n = 22) and digging out of the ground (secondary entrances, n = 8). In all samples it was observed that primary entrances became dome mounds and secondary entrances crater mounds. It is suggested that, although induced airflow (presently, a popular model) may partly explain the presence of mounds, architectural types (dome vs. crater mounds) are the result of energy constraints associated with building materials that differ at the two entrances.

Black-tailed prairie dogs (*Cynomys ludovicianus)* build burrows approximately 12 cm in diameter, 10–30 m long, and 1–5 m deep with two or three entrances (Sheets et al. 1971). Entrances are encircled by conspicuous mounds of soil that may reach 1 m in height and 2.5 m in diameter (King 1955). Both King (1955) and Sheets et al. (1971) describe two distinct types of burrow mounds (Fig. 1): (1) the dome mound, having a wide base and rounded profile; and (2) the crater mound (after Vogel et al. 1973), which has steep walls that rest on a relatively narrow foundation.

Vogel et al. (1973) demonstrated that the energy needed to ventilate an extensive burrow system can be derived from the velocity gradient created at the entrances when mounds differ in height and design. However, adequate airflow can be achieved with only one mound and another bare entrance (Vogel et al. 1973). The presence of a second mound is explained by hypotheses (which they attribute to King 1955) suggesting that mounds at each entrance are needed as antipredator lookouts (vantage points; Hoogland 1979, 1981) and as flood prevention measures (Bailey 1905). I argue that dome and crater mounds represent functionally identical structures that are built under different constraints in transport costs (energy expenditure).

METHODS

Observations were made during a three-year (1981–1983) study in a small (>10 ha) expanding prairie dog colony (Cincotta et al. 1988) in Badlands National Park, South Dakota. In 1981 sites were flagged where prairie dogs were observed (1) digging down into the ground (building a primary entrance) to initiate a burrow (n = 22) and (2) digging out of the ground (a secondary entrance; n = 8). Mound building was monitored during the next three years using 8x binoculars from vantage points outside the colony from May to September and during annual winter visits (one week in January).

RESULTS AND DISCUSSION

Within the sample I observed that mounds encircling primary entrances always became dome mounds. These were composed entirely of subterranean soil spread widely over the ground surrounding the entrance. To form a dome mound, prairie dogs kicked soil from the interior of the burrow into a pile outside the entrance. Then they arranged the material in a dome encircling the entrance hole by pushing this soil and sizable stones (up to 6 cm in diameter) in front of their forepaws, which were held tightly together.

Crater mounds were constructed surrounding secondary entrances. During a period from 11 May to 18 June, each crater mound began as a ring (about 10 cm wide) around the entrance made of uprooted vegetation, displaced litter, humus, and mineral soil. Immediately following the next rain, the prairie dog (or two to four cooperating prairie dogs; Hoogland 1983, King 1955) compacted the

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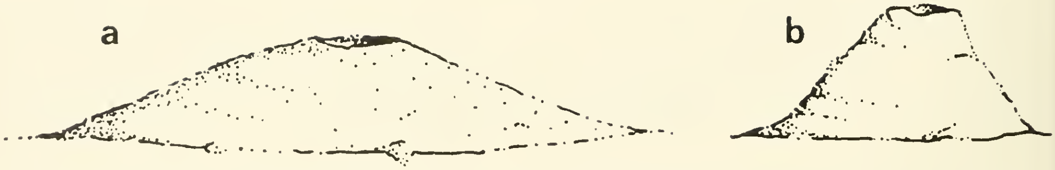

Fig. 1. Depictions of two distinct types of burrow mounds built by black-tailed prairie dogs: (a) the dome mound and (b) the crater mound. Mounds taller than 50 cm are common in older prairie dog colonies.

moist material tightly by pushing against it with its nose (imprints of its nose are generally visible on soil at the mouth of burrows; see Smith 1958), thus giving the mound the strength to stand high on a narrow foundation. Continued quarrying from the adjacent soil surface and subsequent packing resulted in increased height and width and a somewhat conic silhouette that became distinctive over the next two years.

Use of surface materials on secondary entrances can be explained by the fact that when prairie dogs dig their way to the soil surface, they do not have access to excavated subsoil (first noted by King 1955); the bulk of excavated subsoil has already been deposited at the primary entrance. In six secondary entrances, no soil from inside the burrow was deposited around the entrance. Only a handful of dark subsoil was observed near each of the secondary entrances in the two remaining samples.

To use subsoil on secondary entrances, prairie dogs would need to substantially widen tunnels (a poor practice when attempting to restrict predators, especially badgers, *Taxidea taxus;* Cahalane 1950, King 1955, Smith 1958, Koford 1958) or needlessly expend energy in deep excavation and transport. Sheets et al. (1971) report that the tunnel below a crater mound is nearly vertical. Thus, the energy cost of subsoil transport to the surface is high relative to topsoil. In addition, plant fiber available at the surface may bind and stabilize mound soil (prevent cracking and eroding), similar to the manner in which supplemented straw functions in traditional adobe brick construction (McHenry and May 1984). Straw is said to create a more solid adobe brick that dries quickly and uniformly (Boudreau 1971). The inclusion of plant fiber in crater mounds allows prairie dogs to build vertically using less soil (and less energy), thus explaining the characteristic narrow, conical shape of these structures.

I observed that many crater mounds in older parts of prairie dog colonies appeared to have been partially converted to dome mounds, or vice versa. In a survey of mounds (n = 104) in the core of the colony (0.5 ha), representing seven to nine years of prairie dog occupancy, I identified only 52% of mounds as purely domes or craters (see descriptions by King 1955, Sheets et al. 1971, Vogel et al. 1973). Repartitioning of burrows and the impact of predatory badgers are likely the most important causes of these changes.

Both plugging and partitioning of large burrows (Sheets et al. 1971) by dividing coteries or new burrow occupants can sever the connection between entrances (King 1955). If burrows are partitioned, occupants may require additional tunnels and entrances to facilitate fast access and escape from the burrow. Consequently, if tunneling is commenced near an old crater mound, it may become a dumping ground for newly excavated subsoil and may thus develop some of the characteristic shape of a dome mound.

Likewise, badgers often destroy mounds and widen tunnels. I noted three separate instances in which badgers impacted burrows in the colony. In two of the cases excavated soil was pushed back into the burrow after the badger had left the colony, and the tunnel was narrowed to near its original width. Remaining soil around the entrance was repacked to form a somewhat crater-shaped mound. In the third case the entrance was plugged.

CONCLUSION

The ventilation hypothesis (Vogel et al. 1973) does not provide a full explanation of observed mound construction in black-tailed prairie dogs. However, the model presented here is not an alternative to that hypothesis; both models can be evoked simultaneously. The model suggested in this note has its appeal in parsimony, in its consistency with other behavioral observations of "anti-predator alertness" in prairie dog colonies (Hoogland 1981, Loughry 1987), and in its focus on an engineering practice that may reduce energy expenditure.

ACKNOWLEDGMENTS

Field study was sponsored by a grant from the National Park Service (Contract No. CX1200-1-B035) and logistic support from the USDA Forest Service Forest and Range Experiment Station in Rapid City, South Dakota. I thank Superintendent Gil Blinn, Chief Ranger Lloyd Kortje, District Ranger Mike Glass, and the staff of Badlands National Park for their help. I also thank Dan Uresk and the U.S. Forest Service Experiment Station technical staff for their technical assistance. In addition, William Agnew and Deborah Paulson made observations that contributed to my perceptions of prairie dog behavior. Preminda Jacob provided valuable editorial assistance. I dedicate this paper to Professor Emeritus Richard Hansen for the sense of naturalistic curiosity he encouraged in all of his students.

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LESSER PRAIRIE-CHICKEN NEST SITE SELECTION AND VEGETATION CHARACTERISTICS IN TEBUTHIURON-TREATED AND UNTREATED SAND SHINNERY OAK IN TEXAS

D. A. Haukos[1] and L. M. Smith[1]

ABSTRACT.—Radiotelemetry was used to evaluate lesser prairie-chicken (*Tympanuchus pallidicinctus*) nesting response to herbicidal conversion of sand shinnery oak (*Quercus havardii*) rangeland to grassland. Hens selected nest sites in residual grasses within lightly grazed sand shinnery oak habitat with > 75% vertical screening in the first 0.33 m and 50% overhead cover.

Lesser prairie-chicken (*Tympanuchus pallidicinctus*) range has declined > 90% since the late 1800s (Taylor and Guthery 1980). This species is currently restricted to areas in Colorado, Kansas, Oklahoma, New Mexico, and west Texas that are dominated by sand shinnery oak (*Quercus havardii*), sand sagebrush (*Artemisia filifolia*), and short- and mid-prairie grasses (Jones 1963, Taylor and Guthery 1980).

Tebuthiuron (N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N′-dimethylurea) has been used to convert sand shinnery oak–dominated rangelands to short- or mid-prairie grass rangelands. Tebuthiuron has decreased sand shinnery oak densities by 85% (Doerr 1980), and grass yields have increased 300–900% (Pettit 1979). The effect of this conversion on lesser prairie-chicken populations is unknown. The objectives of this study were to ascertain habitat use by nesting female lesser prairie-chickens and to measure vegetation characteristics at nest sites in tebuthiuron-treated and untreated sand shinnery oak habitat.

Fieldwork was conducted 35 km north of Plains, Texas, in Cochran and Yoakum counties, during spring 1987–88. The area studied includes 4,145 ha of rangeland of which an area of 2,331 ha was treated in the late 1970s with tebuthiuron (0.56 kg/ha) in one contiguous block. The primary land use is cattle production. Short- and mid-grasses once codominated the area with sand shinnery oak but have been partially replaced by shinnery oak. Less frequent occurrences of sand sagebrush, sand dropseed (*Sporobolus cryptandrus*), and purple three-awn (*Aristida purpurea*) are interspersed with a variety of forbs (Pettit 1979). Mean annual precipitation is 43 cm, of which > 80% occurs during thunderstorms from May through October (Dittemore and Hyde 1960).

Female lesser prairie-chickens were captured with walk-in traps or rocket nets on leks during spring (March–April 1987–88) display periods (Haukos et al. 1990). Captured hens were fitted with either solar-powered backpack transmitters (Brander 1967) or battery-powered poncho-mounted transmitters (Amstrup 1980). Nests were located by following radio-marked hens. Chi-square analysis with Yates correction for single degree of freedom was used to examine lesser prairie-chicken nest site habitat use (treated vs. control).

At initial nest location, four nest site vegetation characteristics were measured: (1) dominant vegetation type and species at nest site, (2) average vegetation height within 0.5 m of the nest site, (3) percent overhead cover, and (4) vegetation density surrounding the nest site. Percent overhead cover was estimated by averaging two nest canopy cover estimates from 23-mm wide-angle black and white photographs shot from within the nest bowl and overlain with transparent grids (Brown 1962). A profile board (each strata 33 × 15 cm) was used to estimate vegetation density with readings from each cardinal direction at each nest site (Nudds 1977). Readings were taken at a distance of 7 m from the nest site at a height of 1 m (Guthery et al. 1981). Density scores of

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0 (0%), 1 (> 0–5%), 2 (6–20%), 3 (21–40%), 4 (41–60%), 5 (61–80%), 6 (81–95%), and 7 (> 95%) were used; and the scores from each direction were then averaged.

Fifty-five female lesser prairie-chickens were captured on leks and fitted with radio transmitters. All trapped female lesser prairie-chickens selected nest sites in either treated or untreated sand shinnery oak habitat. Due to radio failure, hen predation, and hen emigration from the study area, only 13 lesser prairie-chicken nests were measured.

Of 10 nesting female lesser prairie-chickens captured in treated areas, 8 nested in untreated sand shinnery oak; this was more than expected ($\chi^2 = 4.92$, $P < .05$). All nests found were in residual grasses. Purple three-awn was the dominant vegetation species at the majority of the nest sites (9), followed by little bluestem (*Schizachyrium scoparium*) (3) and sand bluestem (*Andropogon hallii*) (1). Of the measured vegetation characteristics, vertical screening cover and percent overhead cover were the most important features of selected nest sites, presumably for protective cover (Table 1).

TABLE 1. Characteristics of lesser prairie-chicken nests (n = 13) in Yoakum and Cochran counties, Texas 1987–88.

Characteristic	$\bar{x}$	SD
Profile board score		
Strata 1 (0–33 cm)	5.40	1.03
Strata 2 (34–66 cm)	2.59	2.86
Strata 3 (67–99 cm)	0.60	0.60
Overhead cover (%)	42.33	16.24
Plant height (cm)	45.33	10.96

Only two nests were found in treated areas, both of which were in little bluestem. In treated sand shinnery oak, little bluestem provides better vertical screening cover than does purple three-awn. In untreated sand shinnery oak habitat the stems and foliage of oak provide the required vertical screening cover for nest sites, allowing the use of purple three-awn as a nest site.

Sell (1979) recommended that managers provide sand sagebrush and residual grass cover for nesting lesser prairie-chickens. In New Mexico, lesser prairie-chickens preferred ungrazed bluestem grasses, and successful nests were those having greater amounts of cover (Davis et al. 1979). Davis et al. (1979) reported that nest success was greatly reduced in areas of moderate to heavy grazing.

Tebuthiuron treatments of sand shinnery oak in combination with heavy grazing pressure may reduce valuable verticle screening cover needed to provide preferred lesser prairie-chicken nest sites. A grazing schedule and intensity should allow at least 75% vertical screening in the first 0.33 m of cover from ground level and approximately 50% overhead cover to provide nest sites for lesser prairie-chickens in both treated and untreated sand shinnery oak habitats.

ACKNOWLEDGMENTS

The Caesar Kleberg Foundation for Wildlife Conservation and the Houston Livestock Show and Rodeo provided funding for this study. This is contribution T-9-574, College of Agriculture Sciences, Texas Tech University. G. S. Broda provided valuable assistance.

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MOURNING DOVE USE OF MAN-MADE PONDS IN A COLD-DESERT ECOSYSTEM IN IDAHO

Frank P. Howe[1], and Lester D. Flake[1]

ABSTRACT.—Mourning doves (*Zenaida macroura*) in a cold-desert ecosystem used man-made ponds for watering, feeding, gritting, loafing, and courting. Diurnal pond use by doves peaked in the morning and evening. Monthly dove use of ponds fluctuated slightly during the summers of 1984 and 1985. Pond size, pH, and shoreline characteristics had little association with the intensity of pond use by doves; but geographic isolation of ponds was weakly associated with pond-use intensity. The number of doves present at the beginning of the one-hour period was a poor indicator of the number of arrivals during that period. We conclude that man-made water sources are important in areas where water availability may limit mourning dove productivity and abundance. It is suggested that mourning dove arrival rates could be used as a population index in cold-desert areas.

Because many natural water sources are desiccated during the summer, mourning doves (*Zenaida macroura*) in the cold-desert environment of the Idaho National Engineering Laboratory (INEL) depend primarily on man-made ponds for drinking water. They also use the shorelines and peripheral areas of these ponds as feeding, gritting, loafing, and courting sites. Mourning dove use of man-made ponds may vary throughout the day and the breeding season.

Here we report diurnal and monthly watering patterns of mourning doves during the summer in a cold-desert ecosystem and indicate which pond variables are associated with intensity of pond use by mourning doves. We also evaluate the use of rapidly conducted flush counts of doves at pond sites as a predictor of the number of dove arrivals per hour.

STUDY AREA

The Idaho National Engineering Laboratory (INEL) is 80 km (50 miles) west of Idaho Falls on the upper Snake River plain in southeastern Idaho. The INEL encompasses approximately 231,600 ha and is administered by the U.S. Department of Energy. The INEL lies at the northern extent of the Great Basin desert and receives 18–20 cm of precipitation annually (Markham and Halford 1982). Big sagebrush (*Artemisia tridentata*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and a variety of grasses dominate most of the study site; the major vegetation types of the INEL are reported by McBride et al. (1978).

Several man-made ponds are present on the INEL and are used for chemical, sewage, and radionuclide leaching and water overflow. All of the ponds are associated with various research facilities at the INEL. Contaminants in most of the ponds are greatly diluted, and doves regularly use almost all of the ponds as a source of drinking water. More detailed information on the study area is found in Howe and Flake (1988).

Mourning doves on the study site usually nest from mid-May through late August. Dove pairs in southeastern Idaho may complete as many as three nesting cycles during the nesting period (Fichter 1959, Howe and Flake 1989).

METHODS

We collected two separate data sets. The first set involved two ponds at which observations were made several times each month. Data from these intensively monitored ponds yielded information on diurnal and monthly pond use patterns of mourning doves. The second data set involved 10 ponds that were monitored simultaneously on a single occasion each month. We used these data to determine if associations existed between pond use by doves and pond variables. The second data set was also used to determine if the number of doves present at the beginning of a one-hour time period could be used to predict the number of doves that arrived during that hour.

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Intensive Diurnal Dove Counts

Mourning dove pond-use patterns on selected man-made ponds on the INEL were measured by counting the number of dove visits during one-hour time periods. Ponds studied were Argonne National Laboratories–Pond 4 (ANLP4) and Test Reactor Area–Pond 1 (TRAP1) in 1984, and Auxiliary Reactors Area–Pump House (ARAPH) and TRAP1 in 1985; locations and descriptions of these ponds are included in Howe (1986). In 1985 construction and logistical problems at ANLP4 precluded its use as a study pond, and ARAPH was substituted. Midpoints of the five time periods chosen for hourly dove counts were: 0700, 1000, 1300, 1600, and 2100. Ten counts, two per time period, were made each month. Doves were counted in late June, late July, and late August 1984 and in late June, late July, and early September 1985.

Mourning dove visits were separated into two categories: (1) originals—the number of doves flushed when the observer arrived at and walked around the pond, i.e., the number of doves present at the beginning of the one-hour period; and (2) arrivals—the number of doves that arrived during the one-hour period. Category averages were calculated each month. Manpower limitations prevented constant observation of ponds; so 26 all-morning, all-afternoon, and all-evening counts were made to supplement the periodic counts. Data gathered at these ponds were used to determine diurnal and monthly patterns of pond use, expressed as the average number of mourning dove arrivals.

Analysis of variance (ANOVA) (SAS 1985) was used to test for significant differences in the number of dove arrivals between ponds in the same year, among months in the same year, and in the pond-by-month (in the same year) interaction. Fisher's (protected) LSD (Steel and Torrie 1980) was used to compare means among months within the same pond and year at the .05 significance level.

Simultaneous Dove Counts

Ten ponds were surveyed simultaneously from 0930 to 1030 once in June, July, and August of both years. Some chemical leaching ponds were not used by doves and were excluded from the survey. Numbers of original doves flushed at pond sites at 0930 were recorded and compared with the numbers of arrivals from 0930 to 1030. Several technicians and INEL volunteers were used in this portion of the study.

Measurements were made to determine the associations between the intensity of pond use by doves and the following pond variables: shoreline length, length of bare shoreline (bare from the waterline to 35 cm away from the water), slope of shore (from waterline to 1 m away from the water), length of shoreline on other ponds within 1 km, water pH, and the shortest distance to a summer-long water source more than 1 km from the study pond.

Regression analysis procedures (SAS 1985) were used to determine if the number of originals was a good predictor of the number of doves to arrive in the one-hour period (arrivals). Pond variables were compared with the number of arrivals during simultaneous counts using multiple regression analysis procedures (SAS 1985).

RESULTS

Diurnal and Monthly Pond Use

Mourning dove use on three of four INEL ponds peaked twice per day (Fig. 1). We corroborated the pond-use patterns observed during intensive diurnal counts with continuous morning, afternoon, and evening pond observations. Continuous counts indicated that pond use by doves peaked around 0800 and remained high until 1300; this 5-hour period is referred to herein as the morning peak. The number of doves using the study ponds then declined and remained low until about one hour before sunset, when use increased rapidly and reached an evening peak. During the evening peak, the majority of doves arrived from 10 to 30 minutes before sunset and had departed by 20 minutes after sunset; mourning doves did not roost at the ponds. Mourning dove use of TRAP1 was low throughout the summer in 1985, and we detected only minor peaks in diurnal dove use at that pond.

We found that monthly pond use did not vary greatly during the summer on the INEL,

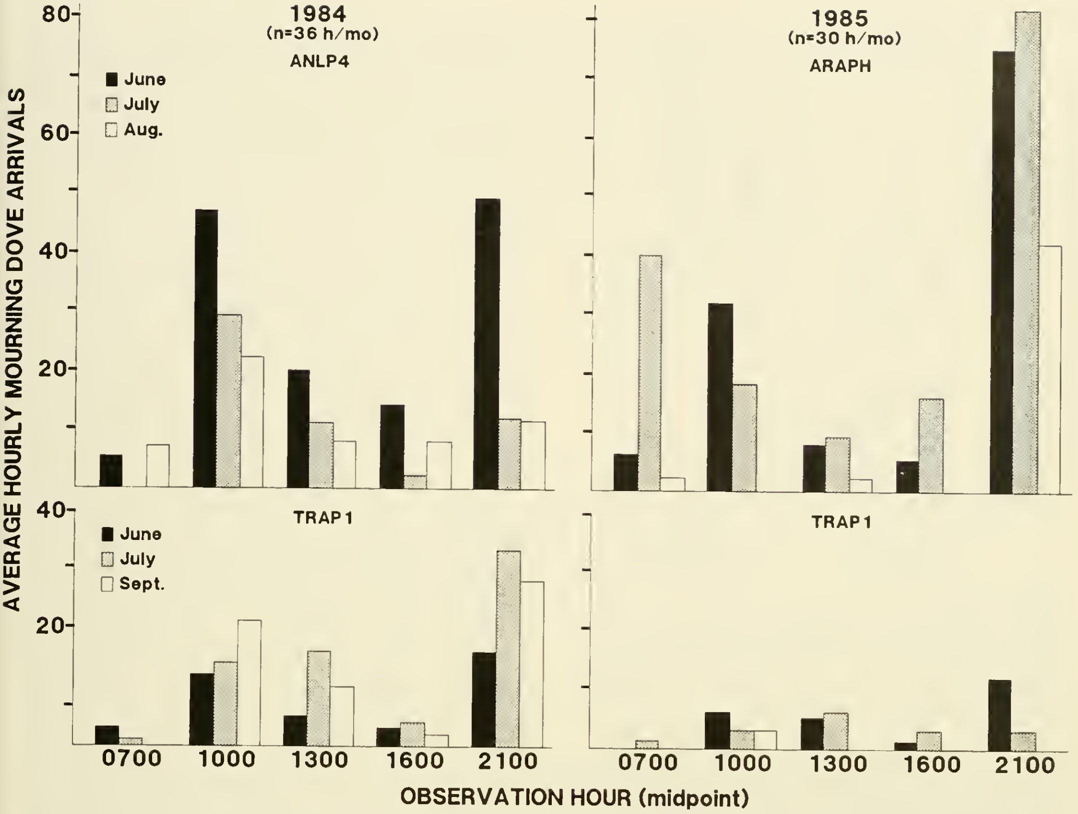

Fig. 1. Diurnal arrival rates ($\bar{x}$ arrivals per hour) of mourning doves at man-made ponds on the Idaho National Engineering Laboratory. Data were gathered in 1984 and 1985 during late June and July, and during late August (1984) or early September (1985). Averages are based on 10 one-hour counts, two counts per time period, five time periods per pond.

with the exception of ANLP4 in 1984. Some temporary fluctuations in dove use did appear and were probably associated with weather. We detected no difference in dove use among months in the same year (F = 2.18; P = .08; 4 d.f.). We did, however, find an interaction of ponds by months in the same year (F = 3.11; P = .02; 4 d.f.); there were more dove arrivals in June 1984 at ANLP4 than during the rest of the summer. This trend was not repeated at TRAP1 in the same year or at either pond in 1985. Also, there were significantly fewer dove arrivals at ARAPH in September 1985 than during the previous months; this trend was repeated (although it was not significant) at TRAP1 in the same year (Fig. 2).

Prediction of Arrivals from Originals

The best model for predicting the number of mourning dove arrivals from the number of originals (doves present at the beginning of the count) had an r^2 value of only .56 at the cubic level (112 d.f.); the r^2 value for the linear model was .38. This implies that one would have little confidence in predicting the amount of pond use using only the number of doves present at the time of observer arrival at the pond.

Pond Variables

Only one of the six pond variables measured was even moderately associated with mourning dove arrivals. Distance to a summer-long water source more than 1 km from the study pond was positively correlated ($r^2 = .49$, $P = .0001$) with the number of mourning dove arrivals.

DISCUSSION

Food, grit, and nesting habitat are readily

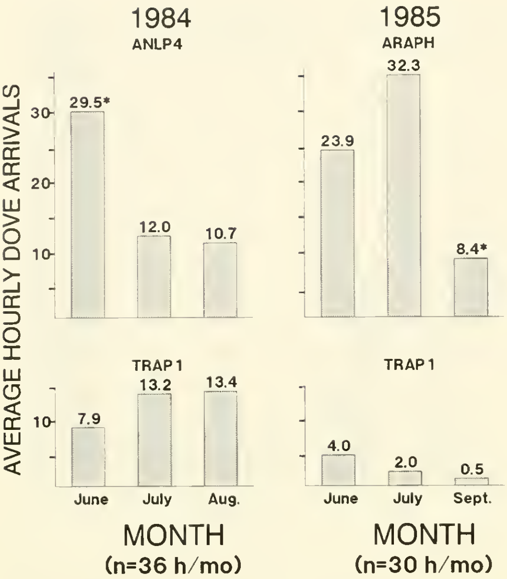

Fig. 2. Hourly mourning dove arrivals by month at selected man-made ponds on the Idaho National Engineering Laboratory. Means from the same pond in the same year marked with an asterisk (*) are different ($P \leq .05$).

available to mourning doves on the INEL (Howe 1986, Markham and Trost 1987, Howe and Flake 1988, 1989), but surface water is limited. Because natural water sources are often dry during the breeding season, we believe that water provided by man-made ponds, ditches, and stock-watering tanks in cold-desert areas such as the INEL may be important to the survival and productivity of mourning doves.

We found morning and evening peaks and a strong mid- to late-afternoon depression in diurnal mourning dove watering patterns. Elder (1956) found that the daily water-use patterns of mourning doves in southern Arizona increased only slightly in the morning and evening. Also, mourning doves on his study site apparently did not exhibit a marked lull in watering activity in the afternoon. He did find, however, that white-winged dove (*Zenaida asiatica*) water-use patterns on the same study site exhibited pronounced morning and evening peaks and an afternoon depression.

Elder (1956) also found that mourning dove use of man-made water sources (game watering reservoirs constructed by the Arizona Game and Fish Commission) was highest from about 1 May to 30 August and steadily declined from early September through late October. The results we obtained were similar, although monthly pond use by doves on the INEL usually peaked later (around 15 May) and declined more abruptly after August. This was to be expected given the difference in latitude between the two study sites.

Mourning dove use of man-made ponds on the INEL fluctuated during the summer but remained comparatively high until early September. We attributed the difference in mourning dove use between early September and late June and July on the ARAPH in 1985 to the seasonal migration of doves. The same trend was seen at TRAP1 in 1985, although the trend was obscured by the low number of doves using TRAP1 in 1985. Mourning dove use of most INEL ponds appeared to be lower in 1985 than in 1984. As no major changes occurred in the pond variables we measured, explanations for the between-year difference in dove use may be related to factors beyond the scope of this study.

We were not able to explain the unusually high number of doves observed at ANLP4 in June 1984. This trend was not evident at the other study pond in 1984 or at either study pond in 1985. Unfortunately, we were not able to determine if the trend was repeated at ANLP4 in 1985 because construction activities and security restrictions precluded its use as a study site that year.

Mourning doves on the INEL usually took less than one minute (one to three draughts) to obtain water; the amount of water uptake in that minute should be enough to satisfy the minimum water needs of a dove for more than a day (Bartholomew and Dawson 1954, MacMillen 1962). Most doves remained from several minutes to more than an hour before and/or after drinking; however, many doves watered more than once a day. Elder (1956) also found that mourning doves remained in the pond areas of his study site for at least 15 minutes before and after watering. Our observations indicated that mourning doves remained in the pond areas to loaf, feed, court, and pick up grit.

Our general observations and statistical results clearly indicated no relationship between pond use by doves and shoreline characteristics (shoreline length, length of bare shoreline, and shoreline slope). Some extremely small water sources, such as seepages, received as much use as ponds several hectares in size. We recorded heavy dove use on the narrow, mud shoreline of one seepage area that was almost entirely covered with emergent cattail. We believe that ponds completely surrounded by emergent vegetation can be greatly improved by opening up several meters of shoreline in one or more spots to allow mourning doves easy access to the waterline. Doves appeared to have no difficulty negotiating steep shorelines.

We believe that distance between ponds may influence dove use. Although doves may travel great distances to water (12.4 km), they generally nest within 3.0 km of their watering sites (Howe and Flake 1988). In cold-desert areas like the INEL, where food and nesting cover are not limited, an even distribution of water sources may enhance dove productivity and/or abundance.

The lack of any strong association between the pond variables and pond use by doves may indicate that some unmeasured factor could have affected dove use of man-made ponds. An alternative explanation is that doves generally used whatever water sources were available, regardless of pond characteristics. We selected pond variables that we felt were logical and meaningful, thus reducing the problems of spurious relationships (Rexstad et al. 1988).

We believe that simultaneous arrival data provide an excellent measure of the value of watering sites for doves; furthermore, we feel that standardized counts of mourning doves at permanent watering sites in desert areas could provide an index of yearly population size.

Acknowledgments

We thank O. D. Markham, T. R. McCabe, K. F. Higgins, and C. G. Scalet for comments and suggestions on this project and/or manuscript. We also thank W. L. Tucker for assistance in statistical design and analysis. We are obliged to our technicians and volunteers for assistance in the collection of data. Funding was provided by the Office of Health and Environmental Research, U.S. Department of Energy, and was a contribution of the INEL Radioecology and Ecology Program. Field support was provided by the U.S. Department of Energy Radiological and Environmental Sciences Laboratory.

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RADIO TRANSMITTER ATTACHMENT FOR CHUKARS

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ABSTRACT.—Thirty-seven chukars (*Alectoris chukar*), fitted with conventional poncho-type radio transmitters, were released on Antelope Island in Utah's Great Salt Lake. Twenty-seven removed their radios, averaging three days after release. The remaining 10 died from predation (average 15 days). Twenty-two chukars with pleated and six with harness ponchos were then released. Five of the pleated ponchos were removed (average four days), and 17 resulted in mortality (average two days). All six harness poncho-equipped birds were dead the following day. A consequential laboratory study comparing various attachment methods (conventional, pleated, harness, and "irreversible" flange poncho vs. bellystrap and wingstrap backpack) favored the wingstrap backpack. The effectiveness of 30 conventional ponchos and 30 wingstrap backpacks was compared on game farm chukars. Twenty-nine removed their ponchos within one day. One remained attached throughout the 30-day trial. All of the wingstrap backpacks remained attached with no apparent problems.

The poncho method of radio transmitter attachment has been used successfully for ruffed grouse (*Bonasa umbellus*) (Small and Rusch 1985) and ring-necked pheasants (*Phasianus colchicus*) (Hill and Robertson 1988). Although a certain method of attachment is compatible with one species, it may not work well for another. This has been shown to be true with various species of waterfowl (Joel D. Huener, personal communication).

The objective of this study was to compare poncho vs. backpack radio transmitter attachment for chukars (*Alectoris chukar*).

STUDY SITES

Field observations were of chukars released on Antelope Island in Utah's Great Salt Lake. Laboratory trials were conducted in 45 cm high × 75 cm wide × 90 cm long wire cages at the Brigham Young University avian research laboratory in Provo, Utah. Game farm chukars were housed in a 30 × 30-m run at the Utah Division of Wildlife Resources game farm in Springville, Utah.

MATERIALS AND METHODS

Thirty-seven chukars were fitted with 30-g radio transmitters using the conventional poncho attachment method (Fig. 1). They were released on Antelope Island 25 August 1988. After six days 28 radios were recovered. Twenty-two radios were then attached to chukars using the pleated poncho (Fig. 1) and six using the harness poncho method (Fig. 1); all birds were released 1 September 1988. Failure of each attachment method promoted a small-scale study comparing conventional, pleated, harness, and "irreversible" flange ponchos (Fig. 1) with bellystrap and wingstrap backpacks (Fig. 2) using simulated radio transmitters.

Simulated poncho radio transmitters were constructed from 50 × 70 mm pieces of Lam-a-lite. A 7/16-inch (11.1-mm) hexagonal nut was attached to the lower part (8 mm from the bottom and 16 mm from either side) of each poncho using 20-gauge soft galvanized wire. A 30-cm-long piece of picture-hanging wire was attached to the left front of each poncho using two 3/8-inch (9.5-mm) hog rings. A 24-mm-diameter hole was cut in the upper half (13 mm from the top and either side) of each conventional, harness, and pleated poncho. A 15-mm-long piece of 16-gauge rebar tie wire was folded and then attached with two hog rings to the lower right front of each conventional poncho to help offset the weight of the antenna and to make the total weight equal to that of the wingstrap backpack (26 g). An 18-mm-diameter hole was cut in the "irreversible" flange poncho. Eight 3-mm slits

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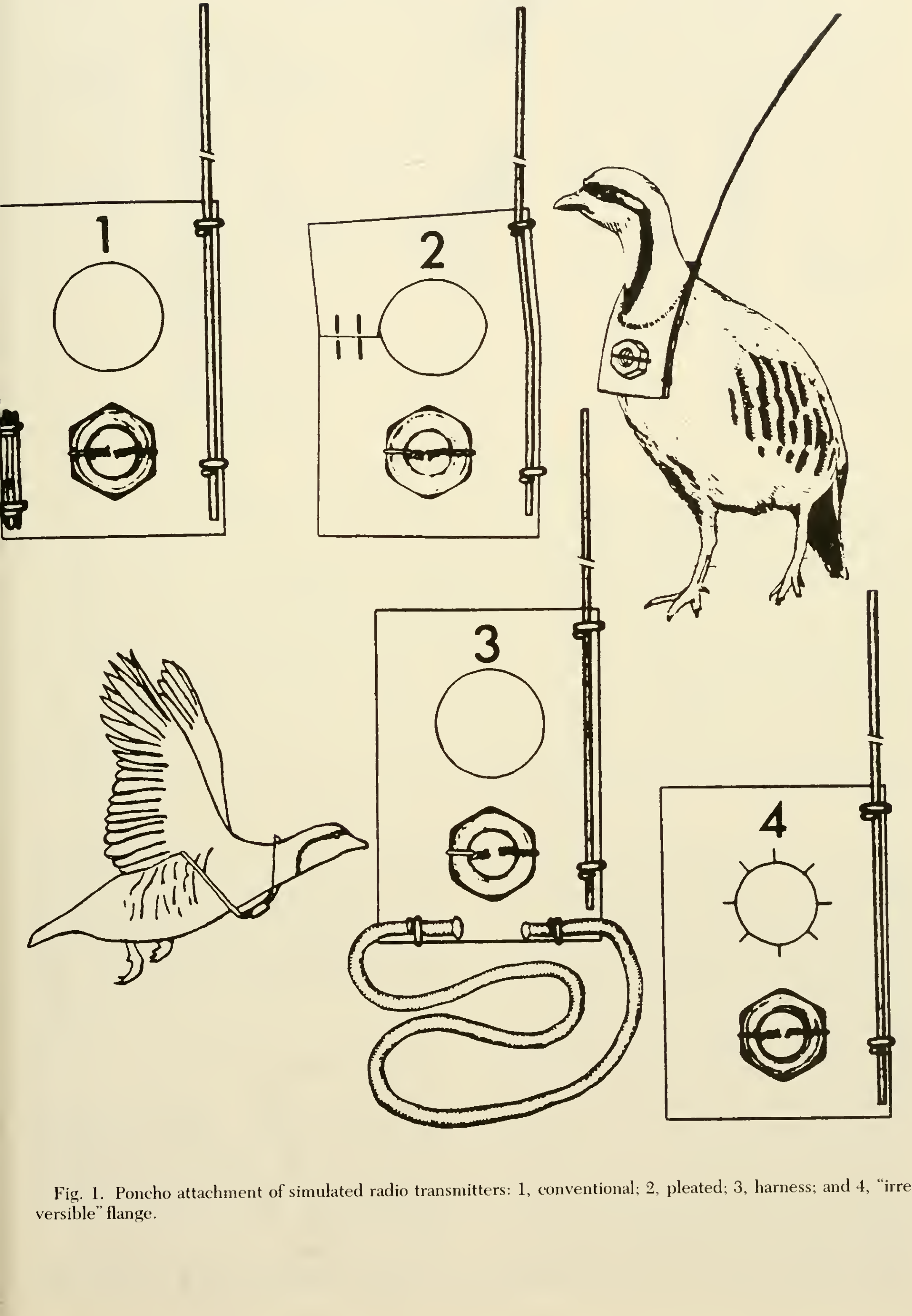

Fig. 1. Poncho attachment of simulated radio transmitters: 1, conventional; 2, pleated; 3, harness; and 4, "irreversible" flange.

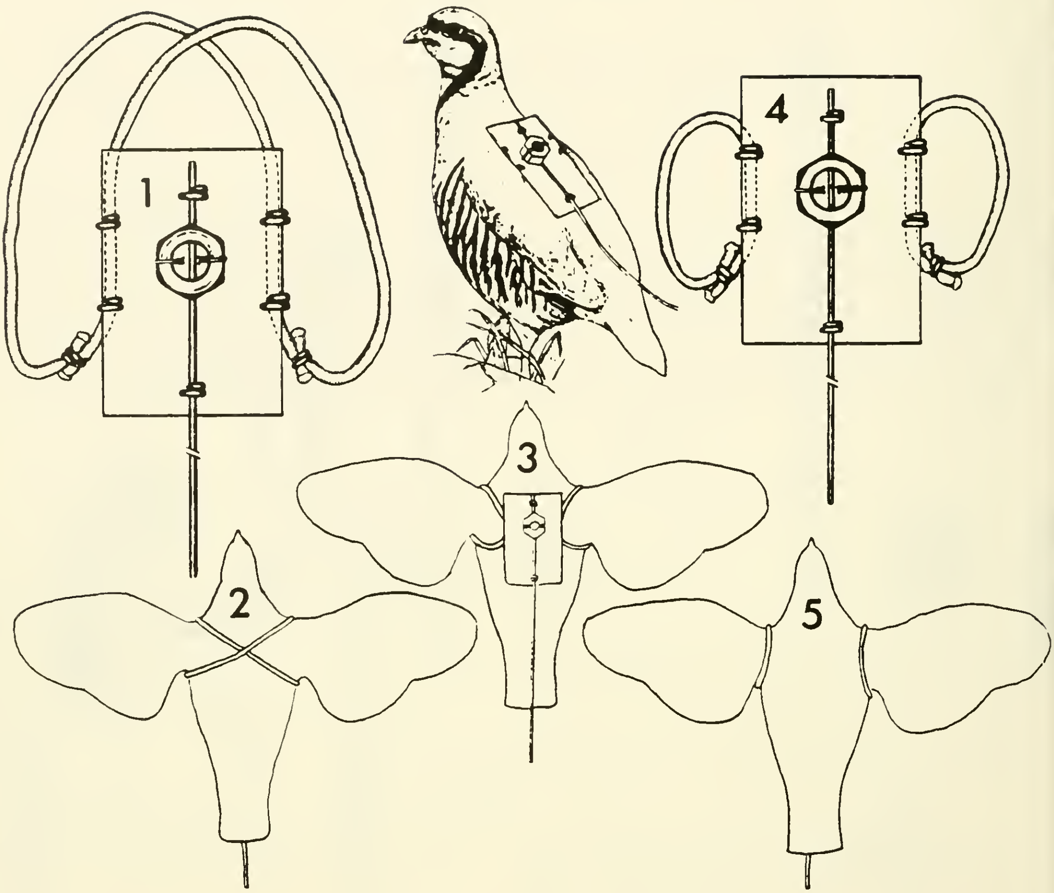

Fig. 2. Backpack attachment of simulated radio transmitters: 1, bellystrap; 2, bellystrap (ventral view); 3, bellystrap or wingstrap (dorsal view); 4, wingstrap; 5, wingstrap (ventral view).

were made to allow the hole to open to 24 mm diameter. A 25-mm-long piece of 3-mm-diameter nylon rope was attached along the bottom of the harness poncho. The rope was looped around the back behind the wings of the bird. The pleated poncho was folded and stapled on the right of the neck hole to reduce the diameter to approximately 20 mm.

Simulated backpack radio transmitters were constructed from 50 × 70-mm pieces of Lam-a-lite. (The backpack design was intended to test the feasibility of attaching poncho radio transmitters as backpacks. A normal backpack attachment would not be as wide.) A 7/16-inch (11.1-mm) hexagonal nut was attached 20 mm from the bottom and 16 mm from each side. A 30-cm-long piece of picture-hanging wire was attached to the center of the front of the Lam-a-lite with two 3/8-inch (9.5-mm) hog rings. A 25-cm-long piece of 3-mm-diameter nylon rope was attached along each side of the bellystrap backpack. The anterior end of the rope on the left side passed under the belly of the bird and attached to the posterior end of the rope on the right side. The anterior end of the rope on the right side passed under the belly and attached to the posterior end of the rope on the left side. The ends were connected using hog rings. A 15-cm-long piece of 3-mm-diameter nylon rope was attached along each side of the wingstrap backpacks using two hog rings. The ropes were looped around the birds' wings and then connected using hog rings.

Picture-hanging wire was not a good choice to simulate antenna wire since, after being

Table 1. Effectiveness of radio transmitter attachment methods on chukars.

Location	Radio transmitter attachment method	Number of birds with radios attached	Number of radios recovered	Recovery condition	Average number of days on bird
Field	Conventional poncho	37	27	off bird	3
			10	mortality	15
	Pleated poncho	22	5	off bird	4
			17	mortality	2
	Harness poncho	6	0	off bird	
			6	mortality	1
Lab	Conventional poncho	2	2	off bird	0
	"Irreversible" flange poncho	2	2	off bird	1[a]
	Harness poncho	2	2	fatigued	1[a]
	Pleated poncho	2	2	fatigued	1[a]
	Bellystrap backpack	2	2	off bird	0
	Wingstrap backpack	2	2	good	14[b]
Game farm	Conventional poncho	30	29	off bird	0
			1	good	30[c]
	Wingstrap backback	30	30	good	30[c]

[a] Transmitters were removed to prevent further injury.

[b] 14-day trial

[c] 30-day trial

bent, it did not return to a straight position. To prevent irritation to the birds, each "antenna" was cut to a length of 15 cm.

Two "radios" of each attachment method were tested for a 14-day period at the Brigham Young University avian research laboratory. Since the wingstrap backpack seemed the most compatible with chukars, a larger study was conducted at the Utah Division of Wildlife Resources game farm to confirm the results of the laboratory trial.

Thirty conventional poncho-type transmitters and 30 wingstrap backpack simulated radio transmitters were fitted to game farm chukars. Although the poncho attachment was not permanent, it was selected for comparison with the wingstrap backpack because it did not result in injury to the birds. For 30 days the birds were monitored to evaluate permanence of attachment, flight ability, and feather wear.

Results and Discussion

Several of the conventional poncho-equipped chukars released on Antelope Island flew for a short distance, struck the antenna with a wing, and then fell to the ground. Others flew well and landed, then began to flip in the air in attempts to remove the radios. Those that were unsuccessful lay for awhile in an exhausted state before trying again. Of the 37 radio-equipped birds (Table 1), 27 removed the radios in an average of three days. The remaining 10 were killed at an average of 10 days following release, quite probably because their fatigued condition made them easy prey.

Of the 22 chukars fitted with pleated ponchos, five were able to remove their radios (average four days). Seventeen were killed or found dead (average two days postrelease). Many had injuries around the neck area, apparently from trying to remove the radios. All of the six harness poncho birds were found dead after one day.

During the laboratory trial, the conventional ponchos, "irreversible" flange ponchos, and bellystrap backpacks were easily removed by the birds within a few minutes following attachment. The pleated and harness ponchos were removed by the researcher after one day because the birds were exhausted and/or injuring themselves. The wingstrap backpack attachment worked well during the 14-day trial with no apparent irritation to the birds.

In the game farm trial, 27 of the birds freed themselves from the ponchos within a few minutes of their attachment. Two more were off by the next morning; only one remained attached for the duration of the trial. All of the wingstrap backpacks remained attached with no indication of irritation to the birds. Flight ability seemed to be unimpaired. Several of the chukars, whose "radios" fit too loosely, showed signs of minor feather wear around the wings.

The results of these studies indicate that chukars are intolerant of attachment to their ventral side. Although the poncho attachment is compatible with other species, the wing-strap backpack appears to be better for chukars. For species on which radio attachment has not been studied, a laboratory trial, preliminary to field study, would be a good precaution.

ACKNOWLEDGMENTS

We express appreciation to Chuck Morris and Stan Andersen (Utah Division of Wildlife Resources), Mitch Larsson and Jim Fillpot (Utah Parks and Recreation, Antelope Island State Park), Curtis Jones, Jerran L. Flinders, Jason Tullis, and Kirsten Slaugh for their assistance with these studies. This research was funded by the Utah Division of Wildlife Resources.

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CHECKLIST OF RECENT MOLLUSCA OF WYOMING, USA

Dorothy E. Beetle[1]

ABSTRACT.—Wyoming lacks a rich molluscan fauna due to its considerable elevation, extremes of temperature, the short period between killing frosts, scanty moisture, and intermittent creeks. Recent mollusks found in the state total 42 genera (109 species), including 6 genera (23 species) of bivalves, 15 genera (42 species) of freshwater gastropods, and 21 genera (44 species) of land gastropods. Synonymy, the counties in which each species was collected, and habitat notes are given.

The state of Wyoming stretches across the Continental Divide. Mountain ranges jut skyward along its western border and run diagonally northwest to southeast across the state. The highest point, Gannett Peak, crowns the Wind River Range at 13,804 feet. The lowest elevation, 3,125 feet, is in the northeast corner of the state in Crook County.

Rivers that flow from these mountains eventually reach the Pacific Ocean or the gulfs of California and Mexico. The Snake River, which flows through Grand Teton National Park, reaches the Pacific Ocean via the Columbia River. The Green River and its tributaries empty into the Colorado River en route to the Gulf of California. Rivers in central and eastern Wyoming eventually join the Missouri River on its way to the Gulf of Mexico.

The climate is rather harsh, with severe winters and mild summers. Minimum winter temperatures may drop to between −40 F and −60 F. Summer days may have comfortable temperatures in the 70s and 80s, but they can go 10 or more degrees higher. Nights are cool. The growing season is restricted, depending upon the elevation, with killing frosts occurring even in May and September on the plains.

Moisture, in the form of rain or snow, is light, ranging from under 22 inches annually in the mountains to 4–6 inches in the Red Desert and along the eastern side of the state. Frost and snow may occur in the mountains even in summer months.

Although it ranks tenth in size among the states, Wyoming lacks a rich molluscan fauna. The extremes of temperature, the short period between killing frosts, the scanty moisture, and intermittent creeks make the state inhospitable to mollusks. Limited habitat is offered on the plains by cottonwoods and willows bordering creeks and ponds, and on steep sedimentary slopes by shrubs. Many of the intermittent creeks disappear in the desert soil. A good many ponds are simply depressions filled by meltwater and are subject to seasonal drying, limiting habitat for freshwater mollusks. Damming of major rivers has changed habitat availability, particularly for bivalves.

Land mollusks occur in greatest abundance and largest number of species in the mountain ranges from the foothills to above timberline. Here moist meadows, aspen stands, willows and shrubs bordering ponds and creeks, and mixed coniferous-deciduous forests offer favorable habitats.

This checklist of Recent Wyoming mollusks gives the counties in which each species was collected as well as habitat data. A total of 42 genera encompassing 109 species and subspecies is listed for the state, including 6 genera (23 species) of bivalves, 15 genera (42 species) of freshwater gastropods, and 21 genera (44 species) of land gastropods. Figure 1 shows the counties outlined in thick lines, the major river drainages indicated by thin lines, and the position of mountain ranges designated by clusters of dots.

Most of the specimens studied were collected on various trips by me between 1948 and 1988 and are in my personal collection. Additional material and/or records were obtained from Stephan L. Welty, Dr. Dwight W. Taylor, Wyoming Game and Fish Commission, Yellowstone National Park biologists,

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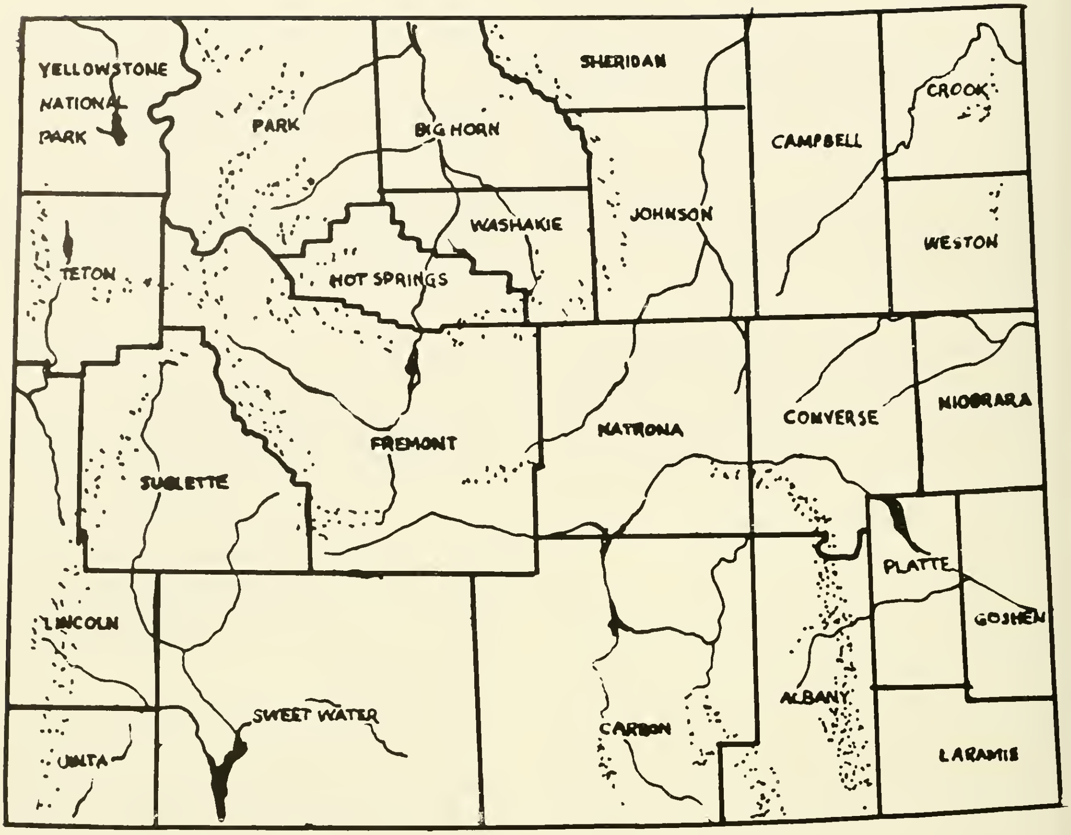
YELLOWSTONE NATIONAL PARK
PARK
BIG HORN
SHERIDAN
CROOK
CAMPBELL
JOHNSON
WASHAKIE
WESTON
TETON
HOT SPRINGS
NIOBRARA
CONVERSE
NATRONA
FREMONT
SUBLETTE
PLATTE
GOSHEN
LINCOLN
ALBANY
SWEET WATER
CARBON
LARAMIE
UINTA

Fig. 1. Wyoming, showing counties, principal rivers, and mountain ranges.

and the University of Colorado Museum at Boulder, Colorado.

CLASS BIVALVIA
Subclass Eulamellibranchia
Order Schizodonta

FAMILY MARGARITIFERIDAE

Margaritifera falcata (Gould, 1850)
County records: Lincoln, Sublette, Teton, Uinta.
Habitat: Streams with sand and cobble bottoms; usually cold water; altitude 6,000–7,000 feet.

FAMILY UNIONIDAE

Anodontoides ferrusacianus (Lea, 1834)
County records: Goshen, Laramie, Platte.
Habitat: North Platte River and its tributaries in sand, silt, and mud; altitude 4,000–6,000 feet.

Anodonta californiensis Lea, 1852
County records: Uinta.
Habitat: Bear River; sand and gravel bottoms.

Lampsilis radiata siliquoidea (Barnes, 1832)
Lampsilis ventricosa (Barnes, 1823)
County records: Converse, Fremont, Natrona, Platte.
Habitat: Sand, gravel and cobble bars in fairly swift water; also silty mud at dams.

Order Sphaeriacea

FAMILY SPHAERIIDAE

Sphaerium lacustre (Muller, 1774)
Sphaerium lacustre ryckholti Normand, 1844
Sphaerium (Musculium) raymondi Cooper, 1892
County records: Albany, Carbon, Fremont, Natrona, Sublette, Teton.
Habitat: In the mud and silt of ponds, small lakes, sloughs, with heavy vegetative growth, or creeks with sandy bottoms; altitude 5,000–9,000 feet.

Sphaerium occidentale (Prime, 1853)
County records: Fremont, Teton.
Habitat: Shallow muddy ponds, depression in a meadow; one occurrence in *Sphagnum* moss edging a bog; altitude 7,000–9,000 feet.

Sphaerium securis (Prime, 1851)
County records: Fremont.
Habitat: Creeks, gravel and mud bottoms with many aquatic plants.

Sphaerium simile (Say, 1816)
County records: Johnson, Sheridan.
Habitat: Perennial bodies of water, usually with a mud or sand bottom and thick aquatic growth.

Sphaerium striatinum (Lamarck, 1818)
Sphaerium tumidum (Baird, 1863)

County records: Albany, Carbon, Goshen, Laramie, Lincoln, Sheridan, Sweetwater, Sublette, Teton, Uinta.
Habitat: Creeks, beaver ponds, small lakes, in mud and vegetation along shore; altitude approximately 4,200–8,000 feet.

Pisidium adamsi Prime, 1852
County records: Teton.
Habitat: In muck of cold, spring-fed pond at 9,650 feet that is briefly ice-free during the summer; in silt and thick plant growth.

Pisidium casertanum (Poli, 1791)
Pisidium concinnulum Sterki, 1906
Pisidium occidentale Newcomb, 1865
Pisidium lucidum Sterki, 1923
County records: Abundant statewide.
Habitat: Ponds, vernal pools, sloughs, marshes, bogs, mud flats, small creeks, and backwaters of rivers; often among roots of plants; in mud; dredged at 35 feet in Lake Marie in the Medicine Bow Mountains, altitude 9,600 feet.

Pisidium compressum Prime, 1851
County records: Albany, Carbon, Goshen, Laramie, Lincoln, Sheridan, Sublette, Sweetwater, Teton, Uinta.
Habitat: Shallow creeks, river and lake margins, sloughs with silt and mud bottoms.

Pisidium contortum Prime, 1851
County records: Albany, Lincoln, Sublette, Sweetwater, Teton, Uinta.
Habitat: Creek margins, ponds; muddy bottom with plants.

Pisidium ferrugineum Prime, 1852
County records: Albany.
Habitat: In muck of beaver pond; altitude 9,100 feet.

Pisidium idahoense Roper, 1890
County records: Teton.
Habitat: Mountain lakes.

Pisidium insigne Gabb, 1868
County records: Lincoln, Sublette, Teton.
Habitat: In mud and plants of overflow from seeps and springs.

Pisidium milium Held, 1836
County records: Fremont, Yellowstone National Park.
Habitat: Small lakes, quiet areas of creeks; mud bottom with plants.

Pisidium nitidum Jenyns, 1832
County records: Big Horn, Carbon.
Habitat: Shallow ponds, sloughs with thick plant growth.

Pisidium obtusale Pfeiffer, 1821
Pisidium obtusale rotundatum Prime, 1851
County records: Sublette, Teton, Uinta.
Habitat: Ponds, sloughs; on mud and roots of aquatic plants.

Pisidium pauperculum Sterki, 1896
County records: Teton.
Habitat: Mountain lake.

Pisidium subtruncatum Malm, 1855
County records: Crook, Lincoln, Sublette, Teton.
Habitat: Shoreline vegetation and mud of creeks, marshes.

Pisidium variabile Prime, 1852
County records: Albany, Carbon, Fremont, Laramie, Sublette, Teton, Uinta, Yellowstone National Park.
Habitat: On plants and mud of ponds and creeks; altitude up to 9,000 feet.

Pisidium ventricosum Prime, 1851
County records: Sublette, Teton, Uinta.
Habitat: Ponds, marshes that do not dry completely.

Class Gastropoda

Subclass Prosobranchia

Order Mesogastropoda

Family Valvatidae

Valvata humeralis Say, 1829
Valvata humeralis californica Pilsbry, 1908
County records: Teton.
Habitat: Lakes, ponds, marsh; mud bottom with thick plant growth.

Valvata sincera Say, 1824
Valvata lewisi Currier, 1868
Valvata lewisi helicoidea Dall, 1905
Valvata sincera helicoidea Dall, 1905
County records: Albany, Teton.
Habitat: Mountain lakes, ponds, a vernal pond, creeks, a bog with thick tan ooze bottom, and heavily vegetated mud bottoms; usually with abundant aquatic vegetation.

Family Hydrobiidae

Lithoglyphus columbiana (Hemphill, 1899)
Fluminicola columbiana (Hemphill, 1899)
County records: Teton.
Habitat: Backwaters of the Snake River.

Lithoglyphus hindsii (Baird, 1863)
Fluminicola fusca (Haldeman, 1847)
Fluminicola coloradoense (Morrison, 1940)
County records: Lincoln, Sublette, Sweetwater, Teton, Uinta.
Habitat: Snake and Green River drainages, on rocks.

Lithoglyphus virens (Lea, 1838)
County records: Lincoln.
Habitat: Rivers, creeks, and irrigation ditches.

Fontelicella robusta Gregg & Taylor, 1965
Amnicola robusta (Walker, 1908)
County records: Lincoln, Teton.
Habitat: Rivers, creeks; on rocks, sticks.

Amnicola greggi Pilsbry, 1935
County records: Lincoln, Sublette, Teton, Yellowstone National Park.
Habitat: Cool springs, spring-fed ponds, on cobbles in river.

Amnicola limosa (Say, 1817)
County records: Teton.
Habitat: Cold spring-fed pond; on silt, gravel, and plants.

Subclass Pulmonata

Order Basommatophora

Family Lymnaeidae

Lymnaea (Fossaria) modicella Say, 1825
Lymnaea humilis rustica (Lea, 1841)
Lymnaea humilis modicella Jay, 1852
County records: Albany, Platte, Sheridan, Teton, Yellowstone National Park.
Habitat: Along water's edge or in shallow water of ditches, swales, creeks; often on mud or moss.

Lymnaea (Fossaria) obrussa Say, 1825
County records: Albany, Big Horn, Converse, Fremont, Goshen, Hot Springs, Johnson, Laramie, Platte, Sublette, Teton, Washakie.

Habitat: Sloughs, marshes, lake edge, ponds that may be temporary, on carcareous algae in warm water spring, cold spring overflow; on mud, silt, gravel, cobbles.

Lymnaea (Fossaria) parva Lea, 1841

County records: Big Horn, Johnson, Lincoln, Sheridan, Sublette, Sweetwater, Teton, Uinta, Washakie, Yellowstone National Park.

Habitat: Sloughs, wet meadows on grass or moss, on wall of moss-lined cave with tiny creek running through it, creek borders in leaves; on sticks and rocks.

Lymnaea (Bakerilymnaea) cockerelli Pilsbry & Ferriss, 1906

County records: Albany, Hot Springs, Laramie, Natrona, Niobrara, Weston.

Habitat: Shallow lakes and ponds that may be temporary, alkali flats around a lake, carbonate crust with algae in overflow from a hot pool.

Lymnaea (Bakerilymnaea) dalli Baker, 1907

County records: Albany, Big Horn, Sheridan.

Habitat: Mountain lakes, cold spring-fed pool; on plants.

Lymnaea (Bakerilymnaea) techella Haldeman, 1867

Lymnaea doddsi Baker, 1911

County records: Albany, Big Horn, Carbon, Fremont, Natrona, Sublette, Sweetwater, Uinta, Washakie.

Habitat: Shallow ponds, slowly flowing creeks; mud, sand, clay bottoms; often with thick algal and plant growth.

Lymnaea (Radix) auricularia (Linnaeus, 1758)

County records: Laramie, Teton.

Habitat: On stones and mud of delta of Arizona Creek.

Lymnaea apressa Say, 1821

Lymnaea stagnalis jugularis Say, 1817

County records: Albany, Lincoln, Sublette, Teton, Uinta, Yellowstone National Park.

Habitat: Ponds (some vernal), stock ponds, lakes, creek margins; mud and saltcrust; usually thick vegetation; altitude 5,000–7,300 feet.

Lymnaea (Hinkleyia) caperata (Say, 1829)

Lymnaea caperata warthini (Baker, 1923)

County records: Widely distributed over the state.

Habitat: Usually occurring in shallow water of vernal ponds, ditches, wet meadows, slowly flowing creeks, and runoff of springs; mud, sand, or clay bottoms; altitude 3,900–9,200 feet.

Lymnaea (Hinkleyia) montanensis (Baker, 1913)

County records: Fremont, Lincoln, Sublette, Teton.

Habitat: Seepage from springs, wet meadows, small creeks; on rocks and plants.

Lymnaea (Stagnicola) catascopium (Say, 1817)

Lymnaea apicina (Lea, 1839)

Lymnaea binneyi (Tryon, 1865)

Lymnaea montana Elrod, 1902

Lymnaea jacksonensis Baker, 1907

Lymnaea (Stagnicola) elrodiana Baker, 1935

County records: Fremont, Lincoln, Sublette, Teton, Yellowstone National Park.

Habitat: Clear mountain rivers and lakes, cold water; on rocks and along water's edge.

Lymnaea (Stagnicola) elodes (Say, 1821)

Lymnaea palustris (Muller, 1774)

Lymnaea palustris nuttalliana Lea, 1841

Lymnaea proxima Lea, 1856

Lymnaea palustris haydeni (Lea, 1858)

Lymnaea traski Tryon, 1863

Lymnaea palustris wyomingensis Baker, 1927

Lymnaea hemphilli (Baker, 1934)

County records: Abundant statewide.

Habitat: Ponds, sloughs, lakes, in almost any aquatic situation; on mud, silt, rocks, vegetation; burrows into mud of vernal ponds; once found completely covering the bottom of a drying sewage pond, once in a saline pond.

Lymnaea (Stagnicola) hinkleyi (Baker, 1906)

County records: Lincoln, Sublette, Sweetwater, Teton, Uinta, Yellowstone National Park.

Habitat: Lakes, rivers.

Pseudosuccinea columella (Say, 1817)

County records: Albany.

Habitat: Small pool, abundant aquatic vegetation.

FAMILY PHYSIDAE

Physa columbiana (Hemphill, 1890)

County records: Teton.

Habitat: On rocks in shallow water of the Snake River.

Physa heterostropha (Say, 1817)

Physa gyrina (Say, 1821)

Physa gyrina aurea (Lea, 1838)

Physa heterostropha aurea (Lea, 1838)

Physa sayi (Tappan, 1839)

Physa virginea (Gould, 1847)

Physa vinosa (Gould, 1847)

Physa ampullacea (Gould, 1854)

Physa triticea (Lea, 1856)

Physa nuttalliana (Lea, 1864)

Physa warreniana (Lea, 1864)

Physa blandi (Lea, 1864)

Physa forsheyi (Lea, 1864)

Physa saffordi (Lea, 1864)

Physa sayi warreniana (Lea, 1864)

Physa cooperi (Tryon, 1865)

Physa propinqua (Tryon, 1865)

Physa wolfiana (Lea, 1869)

Physa walkeri (Crandall, 1901)

Physa smithiana (Baker, 1920)

Physa gyrina smithiana (Baker, 1920)

Physa gyrina gouldi (Clench, 1935)

Physa warreniana gouldi (Clench, 1935)

Physa johnsoni (Clench, 1936)

County records: Widely distributed over the state.

Habitat: Found in a wide variety of situations, mostly in perennial waters; *Physa heterostropha* and *Lymnaea elodes* appear to be mutually exclusive in that where one species is abundant, the other is present in limited numbers or absent.

Physa megachlamys Taylor, 1987

County records: Teton, Yellowstone National Park.

Habitat: Ponds, marshes, lakes with mud substrate and abundant submerged aquatics; on exposed surfaces of logs, stones, and plants.

Physa skinneri Taylor, 1954

County records: Fremont, Lincoln, Sublette, Sweetwater, Teton, Uinta, Yellowstone National Park.

Habitat: Ponds, marshes with plants such as *Typha* and *Scirpus*, ditch, slough off river; mud and silt bottoms; Taylor indicates the species is found in ponds in preference to marshes and at higher elevations and further north than *Physa megachlamys*.

Physa spelunca Turner & Clench, 1974

County records: Big Horn.

Habitat: Limestone cave, in warm-water stream originating from hot spring 1,000 feet from cave entrance; altitude approximately 3,000 feet.

Physa virgata (Gould, 1855)

Physa integra (Haldeman, 1841)

Physa humerosa (Gould, 1855)

Physa anatina (Lea, 1864)

Physa traski (Lea, 1864)

Physa virgata anatina (Lea, 1864)

Physa virgata traski (Lea, 1864)

Physa virgata berendti (Fischer & Crosse, 1886)

Physa utahensis (Clench, 1925)

Physa virgata concolor morph Burch, 1980

County records: South and eastern part of Wyoming.

Habitat: Usually in perennial water such as springs, creeks, and rivers, rather than in lotic situations.

Aplexa elongata (Say, 1821)

Aplexa hypnorum (Linnaeus, 1758)

County records: Albany, Carbon, Converse, Fremont, Platte, Sheridan, Sublette, Sweetwater, Teton, Uinta, Yellowstone National Park.

Habitat: On moss in swampy pastures, adjacent to rivers, sloughs, ponds, (some vernal), ditches with *Typha*, runoff from warm spring; on mud and plants.

FAMILY PLANORBIDAE

Gyraulus circumstriatus (Tryon, 1866)

County records: Albany, Fremont, Lincoln, Platte, Sheridan, Sublette, Teton, Uinta.

Habitat: Ponds, marshes, small lakes, bogs (some drying seasonally), creeks; on wood, rocks, and plants; altitude up to 9,200 feet.

Gyraulus parvus (Say, 1816)

County records: Albany, Big Horn, Campbell, Converse, Fremont, Goshen, Johnson, Laramie, Sheridan, Sublette, Teton (misidentified as *Gyraulus similaris* at mouth of Flat Creek, and as *Gyraulus vermicularis* north of Moran [original site of Moran, at foot of Jackson Lake dam]).

Habitat: Ponds, sloughs, creeks, shallow lakes; usually in heavy vegetation and on stones; mud bottoms.

Armiger crista (Linnaeus, 1758)

County records: Teton, Yellowstone National Park.

Habitat: Seasonal ponds, bog; thick vegetation.

Promenetus exacuous (Say, 1821)

County records: Lincoln, Teton, Yellowstone National Park.

Habitat: Vernal ponds, ditches, small creeks, bogs (one with tan ooze bottom); on waterlilies, *Sphagnum* moss, and other plants; usually a mud bottom; altitude 6,000–7,000 feet.

Promenetus umbilicatellus (Cockerell, 1887)

County records: Albany, Goshen, Johnson, Lincoln, Platte, Teton (specimen from Leigh Lake misidentified as *Gyraulus articus*), Washakie, Yellowstone National Park.

Habitat: Seasonal ponds, sloughs, along stream margins; on plants and rocks; usually a mud bottom; altitude 4,300–8,500 feet.

Planorbula campestris (Dawson, 1875)

Planorbula christyi (Dall, 1905)

County records: Teton.

Habitat: Vernal ponds, bog with tan ooze bottom; thick plant growth.

Helisoma anceps (Menke, 1830)

Helisoma antrosa (Conrad, 1834)

County records: Carbon, Laramie, Platte, Sheridan.

Habitat: Creeks, ditches, ponds; usually a muddy bottom.

Helisoma newberryi (Lea, 1858)

Carinifex jacksonensis (Henderson, 1932)

County records: Teton.

Habitat: Known live only from Jackson Lake; on gravel and silt in shallow water.

Helisoma subcrenatum (Carpenter, 1857)

Helisoma trivolvis subcrenatum (Carpenter, 1857)

Helisoma subcrenatum disjectum (Cooper, 1890)

Helisoma subcrenatum perdisjectum (Baker, 1945)

County records: Fremont, Sublette, Teton, Washakie, Yellowstone National Park.

Habitat: Ponds (some having either cool or warm springs), shallow embayments of lakes, marshes, bogs, small creeks; usually mud substrate with thick aquatic plant growth; burrows into mud of vernal ponds.

Helisoma trivolvis (Say, 1817)

Helisoma trivolvis macrostomum (Whiteaves, 1863)

County records: Carbon, Goshen, Laramie, Niobrara, Teton, Washakie, Yellowstone National Park.

Habitat: Ponds, lakes; usually mud substrate with abundant aquatic plants.

Planorbella duryi (Weatherby, 1879)

County records: Teton.

Habitat: Kelly Warm Spring, temperature 82 F, approximately 100 by 50 feet in size and 4 feet deep. The spring has apparently been the site of release of several species of unwanted tropical fish and snails. The abundance of these animals and the several size classes attest to their successful colonization of the spring.

Planorbella scalaris (Jay, 1839)

County records: Teton.

Habitat: Kelly Warm Spring; see note under *Planorbella duryi*.

FAMILY ANCYLIDAE

Ferrissia rivularis (Say, 1817)

County records: Albany, Carbon, Converse, Fremont, Platte.

Habitat: On rocks and plants (particularly on *Typha* and *Nuphar* stems and leaves), or on dead branches in quiet areas of rivers, creeks, and ponds.

Order Stylommatophora

FAMILY OREOHELICIDAE

Oreohelix carinifera Pilsbry, 1912

County records: Park.

Habitat: Dry slope.

Oreohelix pygmaea Pilsbry, 1913

Oreohelix strigosa berryi Pilsbry, 1915

Oreohelix pygmaea maculata Henderson, 1921

County records: Big Horn, Fremont, Johnson, Sheridan, Washakie, Yellowstone National Park.

Habitat: A mountain species predominantly occupying areas of limestone and sandstone rocks in moist meadows, along creeks under aspen and willow, also under rocks on canyon slopes with sparse stands of shrubs, conifers, and grass; altitude approximately 4,200–8,500 feet.

Oreohelix subrudis (Pfeiffer in Reeve, 1854)

Oreohelix cooperi (Binney, in part, 1869)

Oreohelix subrudis maxima Pilsbry, 1916

Oreohelix subrudis obscura Henderson, 1918

County records: Found in the mountains throughout the state.

Habitat: Preferentially occupies limestone and sandstone areas in aspen, willow, sagebrush, mixed hardwood and conifer stands, in both moist and rather dry places up to timberline.

Oreohelix yavapai extremitatis Pilsbry & Ferriss, 1911

Oreohelix yavapai magnicornu Pilsbry, 1916

County records: Big Horn, Hot Springs, Teton, Washakie.

Habitat: Limestone and sandstone talus, rather dry situations at base of cliffs, under shrubs and grass clumps, occasionally in cottonwood and willow litter in canyons.

Family Sagdidae

Microphysula ingersolli (Bland, 1874)

County records: Albany, Fremont, Sublette, Teton.

Habitat: Aspen and willow leaf litter, on spruce logs in damp places in the mountains.

Family Zonitidae

Euconulus fulvus (Muller, 1774)

Euconulus fulvus alaskensis (Pilsbry, 1899)

County records: Albany, Big Horn, Fremont, Johnson, Laramie, Natrona, Park, Sheridan, Sublette, Teton, Uinta, Washakie, Yellowstone National Park.

Habitat: In litter of aspen, willow, cottonwood, or conifer and moss at seeps and springs; often under dead logs in damp places; an abundant snail of the mountains.

Retinella (Nesovitrea) binneyana (Morse, 1864)

Retinella binneyana occidentalis (Baker, 1930)

County records: Albany, Fremont, Johnson, Sheridan, Sublette, Teton, Washakie.

Habitat: Leaf litter of hardwoods and conifers; edging ponds, creeks, seeps; under limestone rocks in the mountains.

Retinella (Nesovitrea) electrina (Gould, 1841)

County records: Albany, Big Horn, Teton, Uinta, Yellowstone National Park.

Habitat: Leaf litter of willow, cottonwoods, aspen, among sedges; in damp places around sloughs, ponds, and creeks.

Hawaiia minuscula (Binney, 1840)

County records: Albany, Goshen, Laramie, Platte.

Habitat: Under limestone and sandstone rocks on cliffs with sparse juniper and grass; once in willow litter; altitude 4,400–8,500 feet.

Zonitoides arboreus (Say, 1816)

County records: Widely distributed over the state.

Habitat: One of the most abundant land snails, found wherever favorable conditions exist for mollusks; occurs from the base of the foothills to timberline.

Vitrina alaskana Dall, 1905

County records: Found in the mountains throughout Wyoming.

Habitat: In litter of such hardwoods as aspen and willow; in conifer stands; under limestone and sandstone rocks; under logs in moist areas, but also on dry canyon slopes with shrubs and grass from the foothills to timberline at 10,000 feet.

Family Limacidae

Deroceras laeve (Muller, 1774)

Deroceras laeve gracilis (Rafinesque, 1820)

County records: Albany, Big Horn, Fremont, Johnson, Sheridan, Sublette, Teton.

Habitat: Mainly in aspen and willow litter, in moss, around ponds and damp places.

Deroceras reticulatum (Muller, 1774)

County records: Albany, Carbon, Hot Springs, Laramie, Natrona, Sheridan, Washakie.

Habitat: Usually near cultivated places such as gardens, greenhouses, fish hatcheries; in leaf litter and under boards and rocks.

Family Endodontidae

Discus cronkhitei (Newcombe, 1865)

Goniodiscus cronkhitei anthonyi (Pilsbry & Ferris, 1906)

County records: Albany, Big Horn, Carbon, Converse, Fremont, Johnson, Lincoln, Natrona, Park, Sheridan, Sublette, Teton, Washakie, Yellowstone National Park.

Habitat: Abundant in the mountains at 6,000–10,000 feet, particularly in aspen, willow, and mixed associations of lodgepole or limber pine and cottonwood; present in damp situations in *Sphagnum* moss of bogs and seeps; under limestone rocks; in leaves and under logs.

Discus shimeki (Pilsbry, 1890)

Discus shimeki cockerelli (Pilsbry, 1898)

County records: Albany, Big Horn, Fremont, Johnson, Sheridan, Sublette, Teton.

Habitat: Common in mountain canyons, often on the shaded north side in spruce and pine; in willow and meadows along creeks; damp places under logs.

Punctum minutissimum (Lea, 1841)

County records: Albany, Carbon, Natrona, Teton.

Habitat: In the mountains in willow and aspen or spruce in damp places under decaying logs and leaves.

Family Succinidae

Possibly several species of the genera *Oxyloma*, *Succinea*, and *Catinella* exist in Wyoming, but further anatomical work is needed before specific limits can be established. Species previously published by various authors as being present in the state are:

Oxyloma retusa (Lea, 1834)

Oxyloma haydeni (Binney, 1858)

Oxyloma decampi gouldi (Pilsbry, 1948)

Succinea avara (Say, 1824)

Succinea grosvenori (Lea, 1857)

Succinea stretchiana (Bland, 1865)

Catinella avara (Say, 1824)

Catinella wandae (Webb, 1953)

Succineids are found at the edge of ditches, marshes, sloughs, springs, on *Sphagnum* moss of bogs, in leaf and wood debris of willow and aspen. The species that may be *Catinella avara* not only occurs in damp places but has also been found frequently under talus and in crevices of limestone and sandstone cliffs or around the base of shrubs and grass on open slopes. *Succinea grosvenori* has been reported from areas of sparse vegetation, but where the ground may remain somewhat damp.

Succineids have been found in all but four counties in Wyoming: Campbell, Carbon, Park, and Sweetwater.

Family Pupillidae

Gastrocopta armifera (Say, 1821)

County records: Platte.

Habitat: Sandstone and limestone cliffs edging Guernsey Reservoir, under pine and juniper logs; very dry.

Pupoides hordaceus (Gabb, 1866)

County records: Platte.

Habitat: Sandstone and limestone cliffs edging Guernsey Reservoir, under pine and juniper logs; very dry.

Pupilla blandi Morse, 1865

County records: Albany, Converse, Fremont, Goshen, Hot Springs, Johnson, Laramie, Lincoln, Sheridan, Teton, Uinta.

Habitat: In aspen, willow, cottonwood, and pine stands in leaf debris or under sedimentary rocks; common in foothills and mountains; altitude 4,200–9,000 feet.

Pupilla hebes (Ancey, 1881)

County records: Albany, Big Horn, Fremont, Johnson, Sheridan, Teton, Washakie.

Habitat: Common in canyons, often under limestone and sandstone rocks; in rock cavities; around the base of shrubs and conifers; also in leaf debris of willow, aspen, and cottonwood; altitude 5,000–9,500 feet.

Pupilla muscorum (Linnaeus, 1758)

Pupilla muscorum xerobia Pilsbry, 1914

County records: Albany, Big Horn, Fremont, Hot Springs (misidentified as *Pupilla syngenes dextroversa*), Johnson, Teton, Washakie.

Habitat: Around decaying logs; in damp leaves; under rocks in aspen, willow, and cottonwood in the mountains; altitude 6,000–9,000 feet.

Vertigo concinnula Cockerell, 1897

County records: Albany, Big Horn, Johnson, Lincoln, Sheridan, Sublette, Teton.

Habitat: Mountains up to 9,000 feet, in aspen and willow thickets along creeks; in moss of swales; under logs in spruce stands on north-facing slopes.

Vertigo elatior Sterki, 1894

County records: Teton.

Habitat: Aspen and willow stands, under logs and in leaves; fairly moist.

Vertigo gouldi (Binney, 1843)

Vertigo gouldi coloradensis (Cockerell, 1891)

Vertigo gouldi basidens Pilsbry & Vanatta, 1900

County records: Albany, Fremont, Sheridan, Teton.

Habitat: Under logs in aspen and willow stands; damp meadows; bogs; in moss; under sagebrush.

Vertigo modesta (Say, 1824)

Vertigo modesta parietalis (Ancey, 1887)

County records: Albany, Big Horn, Carbon, Fremont, Johnson, Sheridan, Teton, Washakie, Yellowstone National Park.

Habitat: A mountain species, altitude 6,000–9,500 feet; under logs, leaf debris in aspen, spruce, and willow; along sloughs, creeks; in moss of seeps; teeth number varies in the same lot, 0–5, one with 6 teeth.

Vertigo ovata Say 1822

County records: Albany, Big Horn, Fremont, Teton.

Habitat: Willow and aspen leaf debris along creeks, bogs; altitude 5,000–7,500 feet.

Columella alticola (Ingersoll, 1875)

County records: Albany, Johnson, Teton, Yellowstone National Park.

Habitat: Spruce and fir, aspen, and willow stands along creeks; in the mountains from about 6,000 to 9,000 feet.

Columella edentula (Draparnaud, 1805)

County records: Albany, Sheridan.

Habitat: Aspen groves in the mountains; a swale on moss.

FAMILY VALLONIIDAE

Vallonia albula Sterki, 1893

County records: Albany, Big Horn, Converse, Fremont, Hot Springs, Johnson, Laramie, Park, Platte, Sheridan, Teton, Washakie.

Habitat: Often under limestone or sandstone rocks in canyons; in pine, juniper, aspen, willow, and cottonwood litter; usually rather dry situations; altitude 4,300–9,600 feet.

Vallonia costata (Muller, 1774)

Vallonia costata montana Sterki, 1892

County records: Albany, Big Horn, Converse, Fremont, Laramie, Lincoln, Park, Sublette, Washakie.

Habitat: In aspen, pine, or juniper stands; under sandstone and limestone rocks; under logs; altitude 4,500–7,000 feet.

Vallonia cyclophorella Sterki, 1892

County records: Widespread throughout the state.

Habitat: Usually in rather dry situations; under logs and limestone and sandstone rocks; at the base of cliffs and in open stands of aspen, juniper, cottonwood; occasionally in willows; once in moss at the edge of a bog; altitude up to 9,000 feet.

Vallonia excentrica Sterki, 1893

County records: Hot Springs, Sheridan.

Habitat: Around grass roots and under plant debris near human habitation.

Vallonia gracilicosta Reinhardt, 1883

County records: Albany, Big Horn, Converse, Goshen, Johnson, Laramie, Natrona, Platte, Sheridan, Teton, Washakie.

Habitat: Dry situations under logs or leaf debris of willow, cottonwood, juniper, aspen; under limestone or sandstone rocks; altitude 4,400–8,000 feet.

Vallonia pulchella (Muller, 1774)

County records: Albany, Fremont, Hot Springs, Platte, Sheridan.

Habitat: In grass of lawns; under rocks and cottonwood logs.

Zoogenetes harpa (Say, 1824)

County records: Albany, Carbon, Laramie, Park, Sheridan, Teton, Yellowstone National Park.

Habitat: A species of the mountains; under logs and leaves in aspen and willow stands; in moss of bogs.

FAMILY CIONELLIDAE

Cionella lubrica (Muller, 1774)

County records: Albany, Teton, Yellowstone National Park.

Habitat: In leaves of aspen and willow; in moss in damp places; under logs; altitude 7,000–8,000 feet.

ACKNOWLEDGMENTS

I am indebted to Dr. Shi-Kuei Wu, University of Colorado Museum, for his advice and encouragement in preparation of this checklist and most particularly for his study of *Physa* material. Biologists of the Wyoming Game and Fish Commission supplied freshwater mollusks collected from 102 sites in the course of crayfish studies between 1985 and 1987. Dr. Wayne Hubert, Wyoming Cooperative Unit, Fish and Wildlife Research, obtained funds needed in preparation of the checklist. Biologists from Yellowstone National Park collected *Physa* specimens from various locations in the park. Stephan L. Welty and Richard E. Pillmore assisted in fieldwork. Dr. Dwight W. Taylor generously sent maps and records of his collections in Wyoming. Nancy E. Brandauer, University of Colorado Museum, kindly read the manuscript and made suggestions. Richard E. Pillmore drew Figure 1.

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HORIZONTAL AND VERTICAL DIAMETER OF BURROWS OF FIVE SMALL MAMMAL SPECIES IN SOUTHEASTERN IDAHO

John W. Laundré[1]

Abstract.—Burrow diameters of five small mammal species, Townsend's ground squirrel (*Spermophilus townsendii*), Wyoming ground squirrel (*S. elegans*), Ord's kangaroo rat (*Dipodomys ordii*), montane vole (*Microtus montanus*), and deer mouse (*Peromyscus maniculatus*), were examined. Burrow cross sections were noncircular for all species with horizontal diameters 1.2–1.6 times wider than vertical diameters. Montane vole and deer mouse burrows were the smallest diameter, burrows of Wyoming and Townsend's ground squirrels were the largest, and kangaroo rat burrows were intermediate. Soil bulk density and texture significantly affected burrow diameters of montane voles and deer mice but not the other three species.

Fossorial and semifossorial mammals rely on their tunnels for a myriad of purposes, including storage of food, protection from predators, and shelter from the environment. Dimensions of burrows, depth, length, volume, and diameter can indicate function; ground squirrels use shallow burrows for summer retreats but rely on deeper ones for winter hibernation (Bartholomew and Hudson 1961, Alcorn 1940, Shaw 1924). Diameter, depth, and/or length can determine a burrow's effectiveness in thwarting predators. The dimensions of a burrow also determine its impact on soil processes (Laundré and Reynolds, in preparation). Thus, data on burrow measurements would increase our knowledge of the life history of fossorial and semifossorial mammals. However, few data on burrow dimensions of small mammals currently exist.

Several researchers have excavated burrows of different small mammal species (Hawbecker 1940, Criddle 1943, Smith 1948, Panuska and Wade 1956, Miller 1957, Anderson and Allred 1964, Reynolds and Wakkinen 1987). Hawbecker (1940) excavated 15 burrows of the Santa Cruz kangaroo rat (*Dipodomys venustus venustus*) but did not measure any burrow dimensions. Several researchers excavated burrows but measured only depth (Criddle 1943, Panuska and Wade 1956, Anderson and Allred 1964). Smith (1948) measured depth and diameter of one plains pocket gopher (*Geomys bursarius*) burrow. Miller (1957) measured depth, length, volume, and diameter of 9 valley pocket gopher (*Thomomys bottae navus*) burrows. Reynolds and Wakkinen (1987) excavated and measured over 70 burrows of four common species in southeast Idaho. They measured maximum depth, volume, and length but did not record burrow diameter. Thus, data on the diameter of burrows of small mammal species are still limited.

To add to our data base on burrow dimensions, I report diameter measurements of burrows for five common burrowing mammals in southeast Idaho.

Study Area and Methods

Data were collected from two regions in southeastern Idaho: the Idaho National Engineering Laboratory Site (INEL), 65 km north of Pocatello, Bannock Co., Idaho, and near Soda Springs, Caribou Co., Idaho. The INEL is a U.S. Department of Energy National Environmental Research Park on the upper Snake River plain. The area is a cool sagebrush desert dominated by sagebrush (*Artemisia* spp.) and grasses. More complete descriptions of the INEL can be found in Harniss and West (1973) and Anderson and Holte (1981).

Study sites near Soda Springs were in three mountain valleys: site 1 was T33N, R43E, Sec. 25; site 2 was T8S, R42E, Sec. 23; and site 3 was T9S, R43E, Sec. 13. Vegetation at the sites varied from a sagebrush-grass mixture to plantings of alfalfa (*Medicago sativa*) and orchard grass (*Dactylis glomerata*).

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TABLE 1. Mean horizontal and vertical diameters, ± SE (n), for the five species studied. Results of analysis of variance comparisons (F and P) among species within the two diameter measurements are at the bottoms of the appropriate columns. Means with the same superscript within a column are statistically similar.

	Horizontal diameter (cm)			Vertical diameter (cm)		
	$\bar{x} \pm$ SE	n	Range	$\bar{x} \pm$ SE	n	Range
Deer mice	6.1 ± 0.5^{b}	18	1.9–10.5	3.8 ± 0.2^{bc}	18	1.5–5.2
Kangaroo rats	7.6 ± 0.8^{ab}	9	5.7–13.2	4.7 ± 0.4^{ab}	9	3.7–7.3
Townsend's ground squirrels	8.0 ± 0.4^{a}	10	6.5–9.6	5.2 ± 0.2^{a}	10	4.3–6.4
Wyoming ground squirrels	7.8 ± 0.3^{a}	41	2.4–12.3	5.6 ± 0.2^{a}	41	1.4–7.3
Montane voles	4.3 ± 0.3	42	1.1–7.3	3.4 ± 0.2^{c}	42	0.5–6.7
F	22.3			17.6		
P	$< .01$			$< .01$		

I measured burrow diameters of five semifossorial rodent species: Townsend's ground squirrel (*Spermophilus townsendii*), Wyoming ground squirrel (*S. elegans*), deer mouse (*Peromyscus maniculatus*), kangaroo rat (*Dipodomys ordii*), and montane vole (*Microtus montanus*). All Townsend's ground squirrel, deer mouse, and kangaroo rat burrows were on the INEL. Burrows of montane voles were on the INEL and site 3 near Soda Springs. Burrows of Wyoming ground squirrels were on all three Soda Springs sites. I randomly selected burrows at each study site and determined species use of selected burrows by visual observations and/or snap trapping.

Burrows were injected with polyurethane foam (Felthauser and McInroy 1983), which forms a rigid, closed-cell cast. Soil covering burrow casts was removed with shovels and/or backhoes. The burrow systems were mapped (Reynolds and Wakkinen 1987) for use in another phase of this study (Laundré and Reynolds, in preparation). The foam casts were then removed and brought to the laboratory. For each burrow system, three locations along the burrow were randomly chosen, and horizontal and vertical diameters of these points were measured with a Vernier caliper. These measurements were averaged and used to represent the whole burrow system.

Average burrow diameters were compared among species with a single classification analysis of variance. For montane voles and Wyoming ground squirrels, burrows from different sites were excavated and measured. Before interspecific comparisons were made, diameter measurements between/among sites within a species were compared with either t-test (montane voles) or single classification ANOVA designs (Wyoming ground squirrels).

Bulk density and soil texture (percent sand, silt, and clay) were measured at most burrow sites. The core technique (Blake 1965) was used to measure bulk density, and the hydrometer technique (Day 1965) was used for soil texture. Burrow diameters were regressed on bulk density and soil texture in multiple regression analyses. Because the sum of the proportions of the three soil separates in any sample totaled 100%, I also calculated simple regression coefficients for each soil separate individually to determine which had the greatest effect on burrow diameter.

All statistical comparisons were calculated with either the Statistics with Finesse® (J. T. Bolding, Box 339, Fayetteville, Arkansas 72702), Biostatistics® (Linscott's Directory, 40 Glen Dr., Mill Valley, California 94941), or Biostat® (Sigma Soft, 1430 Shalanwood Lane, Placentia, California 92670) computer packages.

RESULTS

I excavated and measured 120 burrows (Table 1). Horizontal and vertical diameters did not differ among sample sites for either montane voles or Wyoming ground squirrels. The data were subsequently combined within species. For all species, the horizontal diameter was 1.2–1.6 times wider than the vertical measurement.

Horizontal and vertical diameters differed significantly among the five species (Table 1). Results of multiple range testing (Newman-Keuls) indicated montane voles had significantly smaller horizontal diameter burrows than the other four species. The two species of ground squirrels and kangaroo rats had the largest and most statistically similar diameter

TABLE 2. Mean (± SE) bulk density (g/cm^3) and soil texture of burrow sites for the five species examined.

	Bulk density	Sand %	Silt %	Clay %	n
Deer Mice	1.40 ± 0.03	35.2 ± 4.1	50.3 ± 3.6	14.2 ± 0.9	16
Kangaroo rats	1.32 ± 0.05	45.0 ± 3.8	36.8 ± 2.3	17.9 ± 2.9	8
Townsend's ground squirrels	1.54 ± 0.06	68.2 ± 0.9	27.6 ± 0.7	4.2 ± 0.3	11
Wyoming ground squirrels	1.21 ± 0.03	43.0 ± 2.5	45.4 ± 2.2	11.4 ± 0.8	41
Montane voles	1.39 ± 0.03	41.3 ± 2.4	46.4 ± 2.4	12.2 ± 0.8	43

TABLE 3. Results of regression analyses for the five species examined. The coefficient of determination (r^2), results of significance tests (F), and probability (P) are given for each analysis. Coefficients of determination for simple regression of diameter on bulk density and soil separates are also presented.

	Multiple regression			Simple regression				
	r^2	F	P	r^2 Bulk density	r^2 Sand %	r^2 Silt %	r^2 Clay %	n
HORIZONTAL DIAMETER								
Deer mice	0.67	4.14	.04	+0.04	−0.04	+0.01	+0.59[a]	13
Kangaroo rats	0.45	0.62	.68	−0.07	+0.03	−0.14	+0.02	8
Townsend's ground squirrels	0.42	0.73	.61	+0.03	+0.01	−0.02	+0.13	9
Wyoming ground squirrels	0.04	0.35	.85	+0.02	+0.01	−0.02	+0.01	40
Montane voles	0.59	12.83	<.001	−0.50[a]	−0.50[a]	+0.55[a]	+0.13[a]	40
VERTICAL DIAMETER								
Deer mice	0.07	0.15	>.50	+0.01	−0.01	+0.01	+0.06	13
Kangaroo rats	0.20	0.19	>.50	−0.04	+0.01	+0.01	−0.01	8
Townsend's ground squirrels	0.52	1.10	.46	+0.31	+0.42	−0.34	−0.19	9
Wyoming ground squirrels	0.04	0.41	.80	+0.01	+0.02	−0.02	−0.01	40
Montane voles	0.51	8.94	<.001	−0.42[a]	−0.44[a]	+0.48[a]	+0.10[a]	40

[a] Significant simple regression coefficient at the $P = .05$ level (2-tailed test). The signs preceding the individual coefficients of determination indicate whether the regression slope is positive or negative.

burrows. However, horizontal burrow diameters of kangaroo rats were also statistically similar to those of deer mice.

Vertical diameters of montane vole burrows were statistically similar to deer mice burrow diameters which, in turn, were indistinguishable from diameters of kangaroo rat burrows. As with horizontal diameters, kangaroo rat burrows also had statistically similar diameters to those of the two ground squirrel species.

Bulk density and soil texture (Table 2) varied among species. Multiple regressions of horizontal diameters with bulk density and soil texture were significant for deer mice and montane voles (Table 3). Vertical diameters of burrows regressed significantly only for montane voles. Horizontal and vertical diameters of montane vole burrows significantly regressed separately with bulk density and all soil separates. Bulk density and percent sand had negative effects, and percent silt and clay had positive effects on burrow diameters. Percent clay was the one soil component to regress significantly with horizontal diameters of deer mice burrows.

DISCUSSION

Burrows of the five species examined were not circular or oval in cross section. Rather, the floors of the burrows were flattened, likely by the repeated movement of the burrow occupant through the tunnel.

Burrow diameters corresponded to body size of the five species examined. Deer mice and montane voles were the two smallest species and had the smallest diameter burrows. Kangaroo rats have an intermediate body size, but their burrow diameters were statistically indistinguishable from either the smaller mice or the larger ground squirrel burrows.

As indicated by multiple regression analyses, burrow diameter for the larger species was not affected by bulk density and soil texture. Of the five species, kangaroo rats and ground squirrels are possibly the strongest diggers and would least likely be influenced by soil properties. Montane voles are relatively weak diggers; and, thus, increased soil compaction would most likely limit the diameter of a burrow they constructed. The relationships between burrow diameters of montane voles and soil separates undoubtedly reflect complex combinations of soil properties related to soil texture that affect ease of digging and maintenance of burrow integrity.

ACKNOWLEDGMENTS

The data reported here were collected in concurrence with a study of burrowing dynamics of small mammals funded by a grant to B. L. Keller from the U.S. Department of Energy, Idaho Operations Office, Idaho Falls. I thank W. Bailey, D. Braun, T. Eichholz, D. Hewitt, K. Kunkle, T. Reynolds, M. Restani, D. Sharp, and J. Thompson for their help in the field.

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ECOLOGY OF *COMANDRA UMBELLATA* (SANTALACEAE) IN WESTERN WYOMING

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Abstract.—*Comandra umbellata* is the alternate host of a hard pine canker rust disease induced by the fungus *Cronartium comandrae*. The occurrence and density of *C. umbellata* were recorded near lodgepole pine stands in the Wind River District, Shoshone National Forest, Wyoming. Comandra populations occurred most often on slopes with southern aspects, particularly southwestern, and on steep slopes; these sites tended to be dry and relatively open. Comandra was also found growing under heavy perennial shrub canopy covers. It was most often associated with sagebrush but was common near other perennial shrubs as well. Overall, *C. umbellata* appeared to be a poor competitor with dense grass populations. Comandra was found primarily on *Abies lasiocarpa/Juniperus communis, Pinus flexilis/ Hesperochloa kingii*, and *Artemisia tridentata/Festuca idahoensis* habitats. No comandra was found in the *Abies lasiocarpa/Vaccinium scoporium* habitat.

Comandra umbellata (L.) Nutt. (comandra or bastard toadflax) (Krebill 1968) is a perennial herb of the sandalwood family (Santalaceae). Comandra is a root parasite that forms haustorial connections with over 40 perennial host species (Harrington 1945, Powell 1970), sagebrush (*Artemisia* spp.) being the most common host (Piehl 1965). It is a facultative parasite, meaning it can develop without a host, but plants are much more vigorous when attached to a host (Laycock and Krebill 1967).

Comandra is the alternate host for the hard pine rust disease caused by *Cronartium comandrae* Pk. The fungus produces spore stages on both hosts in order to complete its life cycle and successfully infect the pine. In the West, the major hosts of the fungus are lodgepole pine (*Pinus contorta* Dougl.) and ponderosa pine (*P. ponderosa* Laws.) (Boyce 1961, Johnson 1986). The disease occurs throughout much of the West but is a serious threat to trees only in certain areas, such as the Wind River District of the Shoshone National Forest in Wyoming, where over 50% of the standing lodgepole pine basal area is infected (Geils and Jacobi 1984).

Comandra populations are frequently found near lodgepole pine stands on typically dry and exposed sites that include rocky outcrops. Comandra may be found in grass or fairly dense sagebrush with deeper soils (Laycock and Krebill 1967). However, comandra is only occasionally found in the understory of open pine stands, apparently because it is disadvantaged by deep shade (Krebill 1968). Comandra growth appears to be stimulated by removal of overstory vegetation, but it rarely becomes a dominant member of a vegetation community. Piehl (1965) described *C. umbellata* as inhabiting dry, partially to completely open sites, such as might be found at the top of road cuts or similar clearings.

Knowledge of the alternate host's locations and site requirements is important in understanding the occurrence of the rust disease. It would be useful if specific site characteristics could accurately indicate probable occurrence and relative density or abundance of comandra populations. This knowledge could influence future comandra blister rust management and help in the development of a risk-rating system for lodgepole pine stands. Thus, the objectives of this study were to locate, map, and record site characteristics, occurrence, and amount of *C. umbellata* in portions of the Wind River District, Shoshone National Forest, Wyoming.

Materials and Methods

There are 20,170 hectares of commercial forest land in the Wind River District, with lodgepole pine accounting for almost one-third of the living stems and basal area. Comandra blister rust infection incidence is high in the lodgepole pine, with 50% of all the living stem basal area affected (Geils and Jacobi 1984).

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A survey of comandra populations on nonforested rangeland was completed during the summer of 1983. Sites with various vegetation associations were examined, such as those dominated by (1) sagebrush (*Artemisia tridentata* Nutt.); (2) forbs and grasses, such as *Sedum* and *Festuca;* (3) perennial species other than sagebrush; (4) willow (*Salix* spp.), rabbitbrush (*Chrysothamnus nauseosus* [Pallas] Britt.), and bitterbrush (*Purshia tridentata* Pursh); and (5) sedge species (*Carex* spp.) and grouse whortleberry (*Vaccinium scoparium* [Leiberg] Mazama).

The survey was based on plots approximately 0.3 km long and 0.1–1.5 km wide, with adjustments made to accommodate topographical and vegetational barriers. Each plot was divided into subplots according to slope position, with ridgetop at the crest and upper slope, middle slope, or bottom slope representing equal thirds of the slope. Sites with undulating or flat topography were not divided into subplots and were treated as a separate category. Many plots had only two or three slope positions surveyed because the others were out of rangeland. Data collected for slope position plots included habitat type, dominant plant cover, current vegetation, percent plant cover, plot slope, aspect, rockiness, comandra occurrence, and comandra population index.

Habitat types were classified following Steele et al. (1983). Dominant plant cover was defined as the species occupying the most crown space (land area covered) on a given plot. Current vegetation was divided into three categories: (1) the most abundant species on a plot, which was usually the same as the dominant plant species; (2) the second most abundant species; and (3) the third most abundant species. Percent plant cover was defined as percent of ground covered by plant canopies.

Slope and aspect were taken at midplot. Aspect was broken down into nine subcategories including north, northeast, northwest, south, southwest, southeast, east, west, and flat. Rockiness was defined as the percent of ground surface covered with soil particles greater than 1.27 cm (1/2 inch) in diameter. Plot area and elevation at midplot were determined from USGS topographic maps (7.5-minute quadrangles).

Comandra population occurrence was defined as the presence or absence of *C. umbellata* on any given plot or subplot. Comandra population index for each subplot was determined by counting the number of paces of the surveyor that were "in" comandra populations compared with the total number of paces taken. This procedure gave relative population density ratings for comandra on each plot. Index values ranged from 0 to 10, where 0 had no comandra plants, 1 had 1–15% of the paces in comandra population, 2 had 16–25%, and so on up to 10, where greater than 95% of the paces were in comandra.

Due to the uneven distribution of subplot data, nonparametric analysis from the SPSS statistical package (Nie et al. 1975) was used to analyze comandra plant index information. Friedman's two-way analysis of variance was used to measure differences in comandra population indices among slope positions. Kruskal-Wallis one-way analysis of variance was used to determine if any plot variables, such as slope or aspect, were significant predictors of comandra density indices. Chi-square tests were utilized to determine significant differences between observed and expected values for comandra occurrence as predicted by site variables.

RESULTS AND DISCUSSION

During this study, 152 possible comandra plant sites were surveyed encompassing nearly 6,200 ha of rangeland adjacent to, or located within, forested areas. Eighty-three plots had comandra, thus accounting for 48% of the total area surveyed and 55% of the total number of sites surveyed. The lowest elevation at which *C. umbellata* was mapped in our study was 2,316 m, but undoubtedly it is present at somewhat lower elevations. The highest elevation site containing comandra was 2,865 m, the highest known population of *C. umbellata* in Wyoming (Dittberner and Olson 1983).

EFFECT OF ASPECT.—The variable that had the strongest positive correlation with the occurrence of comandra populations was aspect. Data indicated that southern aspects were most common for sites surveyed in the Wind River District (Table 1); of these plots, 80% had *C. umbellata*, and nearly 55% faced southwest. Southern aspects were more

TABLE 1. Effects of slope aspect on *Comandra umbellata* occurrence.

Aspect[1]	Total no. plots[3]	Plots with comandra		
		No.	Expected value	%
Northern	33	4	18.4	12
Southern	91	66	50.7	72
Western	5	3	2.8	60
Flat[2]	20	10	11.1	50
Plot totals	149	83		
Total chi-square[4]	36.14*			

[1] Aspect was established as degrees from true North (360°): northern was from 315° to 45°, eastern from 45° to 135°, southern from 135° to 225°, and western from 225° to 315° from true North.

[2] Flat aspects were assigned to those subplots not having a dominant aspect, such as found on undulating topography.

[3] Does not include three plots with eastern aspects.

[4] Total chi-square value is the sum of cell chi-square of plots with and without *C. umbellata*. Northern plots with comandra contributed 31%, and northern plots without comandra contributed 39% to the total chi-square.

*Indicates significant differences from expected values at $p \leq .05$.

TABLE 2. Effects of percent slope on *C. umbellata* occurrence.

Percent slope classes[1]	Total no. plots	Plots with comandra		
		No. plots	Expected value	%
0%	51	20	27.8	39
1–25%	57	23	31.1	40
26–50%	38	35	20.8	92
> 50%	6	5	3.3	83
Total no. plots	152	83		
Total chi-square[2]	31.99*			

[1] Percent slope was determined at midplot for each plot surveyed.

[2] Total chi-square value is the sum of cell chi-squares of plots with and without *C. umbellata* in each class. The 26–50% class with comandra contributed 29%, and the 26–50% class without comandra contributed 30% of the total chi-square.

*Indicates significant difference from expected values at $p \leq .05$.

exposed and the vegetation sparser. The parasitic and associative nature of *C. umbellata* may be better adapted to such sites than to less exposed sites. Kruskal-Wallis analysis showed, however, that aspect did not influence relative population density indices.

EFFECTS OF SLOPE.—Comandra populations seemed to have a higher probability of occurring on sites with slopes greater than 25% since 92% of these sites had comandra (Table 2). It should be noted that the number of plots with and without comandra in the first two slope classes was similar. Percent slope did not significantly affect the relative density of comandra populations.

EFFECTS OF SLOPE POSITION.—Comandra occurrence did vary significantly among topographic positions (i.e., ridgetop, upper, middle, and bottom positions) according to chi-square tests (Table 3). Friedman's two-way analysis of variance tests indicated that when comandra was present on a site, bottom slope positions tended to have significantly lower population density indices than other positions (Table 3).

HABITAT TYPE RELATIONSHIPS.—The following habitat types were found in the study area: (1) *Abies lasiocarpa/Juniperus communis* (Abla/Juco), (2) *Pinus flexilis/Hesperochloae kingii* (Pifl/Heki), (3) *Artemisia tridentata/Festuca idahoensis* (Artr/Feid), (4) *Abies lasiocarpa/Vaccinium scoparium* (Abla/Vasc), and (5) miscellaneous habitat types. Chi-square tests detected significant differences in occurrence of comandra among these habitat types (Table 4).

The Abla/Vasc habitat type contributed most to the overall chi-square value because none of the plots had comandra. Seventy percent of the plots with comandra occurred on Abla/Juco, Pifl/Heki, or Artr/Feid habitats. The Artr/Feid habitat type had less comandra than all other types with comandra. Grass species, particularly *Festuca idahoensis*, were often quite abundant within this habitat. Comandra was not found in association with dense grass populations but was commonly associated with sparse and clumpy grass populations. Three plots (12%) of the

TABLE 3. Effects of slope position on *Comandra umbellata* occurrence and population indices.

Slope position (subplots)	Total no. subplots[2]	Subplots with comandra			Mean comandra index[3]	Friedman's analysis[1]
		No.	Expected value	%		
Ridgetop	51	36	29.4	81	2.7	a[4]
Upper	43	33	24.8	77	3.8	a
Middle	84	53	48.4	63	3.3	a
Bottom	100	31	57.6	31	1.0	b
Undulating	19	18	10.9	95	1.8	–
Totals	297	171	171.1		2.5	
Total chi-square[5]	50.71*					

[1] Friedman's two-way analysis of variance tests were used to compare the effects of slope position on *C. umbellata* population density indices.

[2] Total numbers of subplots for each slope position are not equal because each plot did not have all slope positions present.

[3] Comandra population index was based on the mean percent of paces in *C. umbellata* for each slope position with comandra. The mean percent was divided by 10 to obtain an index value.

[4] Means of comandra population indices with a common letter were not significantly different at p .05. Undulating slope positions were not included in Friedman's two-way ANOVA tests due to a small number of cases where an actual two-way analysis could be made.

[5] Chi-square analysis was used to test for uniform distribution of slope positions. Chi-square analysis tested all slope positions with *C. umbellata* against all slope positions without *C. umbellata*.

*Indicates significant differences from expected values at $p \leq .05$.

TABLE 4. Relationship of habitat types and *Comandra umbellata* occurrence.

Habitat type	Total no. plots	Plots with comandra		
		No.	Expected value	%
Abies lasiocarpa/ Juniperus communis	43	25	23.5	58
Pinus flexilis/ Hesperochloae kingii	28	22	15.3	79
Artemisia tridentata/ Festuca idahoensis	32	11	17.5	34
Abies lasiocarpa/ Vaccinium scoparium	20	0	10.9	0
All other habitat types[1]	29	25	15.8	86
Total	152	83		
Total chi-square[2]	47.73*			

[1] Includes five habitat types: (1) *Pseudotsuga menziesii/Juniperus communis*, (2) *Picea engelmannii/Equisetum arvense*, (3) *Pinus contorta/Juniperus communis*, (4) *Festuca idahoensis/Carex* sp., and (5) unclassified.

[2] Total chi-square is the sum of cell chi-squares of plots with and without *C. umbellata*. Abla/Vasc with comandra contributed 23%, and Abla/Vasc without comandra contributed 28% of total chi-square.

*Indicates significant differences from expected values at $p \leq .05$.

Festuca idahoensis/Carex spp. habitat types had comandra.

The miscellaneous habitat category had no distinguishable pattern regarding type of habitat favoring comandra development. Eighty-four percent of these 25 plots were in *Pseudotsuga menziesii/Juniperus communis*, *Picea engelmannii/Equisetum arvense*, or *Pinus contorta/Juniperus communis* types.

The Kruskal-Wallis tests did not show significant differences among comandra population indices on locations with different habitat types. Thus, habitat typing might prove useful in predicting comandra occurrence but not in estimating abundance. In general, comandra plants were found in most of what may be considered the drier plant habitat types where grass was not dominant, and rarely in moister habitat types.

DOMINANT PLANT AND CURRENT VEGETATION RELATIONSHIPS.—Sagebrush (*Artemisia tridentata* Nutt.) was by far the most common species encountered. Seventy-three (88%) of the 83 plots with comandra had sagebrush as the dominant species or the most common "current vegetation." Fifty-four of these plots had Idaho fescue (*Festuca idahoensis* Elmer.) as the second most common species. Beyond

TABLE 5. Effects of percent plant canopy cover on *Comandra umbellata* occurrence.

		Plots with comandra		
Percent plant canopy cover classes[1]	Total no. plots	No.	Expected value	%
0–25%	6	6	3.3	100
26–50%	20	16	10.9	80
> 50%[2]	126	61	68.8	48
Plot totals	152	83		
Total chi-square[3]	12.14*			

[1] Percent plant canopy cover was defined as the percent of the ground covered by plant canopies.

[2] The > 50% class was used instead of 51–75% and 76–100% because it was difficult to visually distinguish between the latter two categories.

[3] Chi-square analysis tested all classes with *C. umbellata* against all classes without *C. umbellata*. The 0–25% and 26–50% classes with *C. umbellata* contributed 38%, and those without *C. umbellata* contributed 40% of total chi-square.

*Indicates significant differences from expected values at $p \leq .05$.

this, current vegetation categories were indistinct in the analysis. Sagebrush was a useful indicator in locating comandra; however, other perennials apparently served as hosts. Wood rose (*Rosa woodsii* Lindl.), stone crop (*Sedum stenopetalum* Pursh.), bitterbrush (*Purshia tridentata* Pursh.), and rabbitbrush (*Chrysothamnus nauseosus* Nutt.) were found in association with comandra populations and probably served as hosts.

Our findings are similar to those of Laycock and Krebill (1967), who found comandra often in association with sagebrush on open, dry sites with rocky outcrops. Although they found *C. umbellata* under dense sagebrush and in grass, they did not describe possible adverse effects of thick grass populations. Piehl (1965) also found comandra inhabiting dry, partly or completely open sites, but did not mention its ability to grow under dense sagebrush populations.

PLANT CANOPY COVER RELATIONSHIPS.— Because comandra tends to be a poor competitor (Krebill 1968), it seemed reasonable to assume that open sites would permit its establishment and growth. Survey results indicate this assumption may not always be reliable if the survey unit is a large area. Significant differences of plant canopy coverage between expected and observed number of plots with and without comandra were observed with chi-square tests (Table 5). Comandra populations occurred most commonly within plots and subplots having more than 50% of the ground covered by plant canopies. However, the heavily vegetated class contributed little to the total chi-square value, as 65 plots in this class lacked comandra. Greater contributions were made by lower percent cover classes where more plots had comandra than not. In most cases, vegetation in the Wind River District tended to cover 51–100% of the ground surface.

Interpretation of these results may be misleading in that whole subplots were surveyed according to percent canopy cover, whereas comandra populations occurred in patches throughout the subplot. Comandra was found where grass cover was minimal, but abundance of perennial hosts varied widely. This occurred where grass clumps were associated with comandra under thick sagebrush or woody shrub canopies.

In a comparison of percent canopy cover within each slope position class, Kruskal-Wallis analysis of comandra population indices showed no significant differences, except on bottom slopes where there was less comandra.

Most plots with comandra were in the moderate and heavy classes for rockiness. Differences occurred between the observed and expected values when comparing plots with *C. umbellata* to those without. Most of the differences can be attributed to the small number of observations in the light rockiness class. Most of the rangeland surveyed was in the moderate and heavy rockiness classes. Therefore, rockiness was not an adequate predictor of comandra presence or of comandra plant index.

The results of this study give a good indication of where comandra populations can be found in the Wind River District. The association of comandra occurrence with certain slopes, aspects, habitat types, and plant associations can be used by pathologists and forest managers in predicting and managing comandra rust disease.

ACKNOWLEDGMENTS

We thank J. R. zumBrunnen of the Statistical Laboratory, Colorado State University, for statistical advice. Research was supported by Colorado Agricultural Experiment Station—McIntyre Stennis Funds No. 15-5013.

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The Great Basin Naturalist

VOLUME 49, 1989

EDITOR: STEPHEN L. WOOD

THE GREAT BASIN NATURALIST
BYU PROVO, UTAH
1939

PUBLISHED AT BRIGHAM YOUNG UNIVERSITY
BY BRIGHAM YOUNG UNIVERSITY

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6829

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